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Ecology and Conservation of the Montane Forest Avian Community in Northeastern North America

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ECOLOGY AND CONSERVATION OF THE MONTANE FOREST AVIAN COMMUNITY IN NORTHEASTERN NORTH AMERICA

A Dissertation Presented

by

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ECOLOGY AND CONSERVATION OF THE HIGH ELEVATION FOREST AVIAN COMMUNITY IN NORTHEASTERN NORTH AMERICA

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DEDICATION

To Allison, this dissertation simply would not have been possible without your love, support and friendship.

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ABSTRACT

ECOLOGY AND CONSERVATION OF THE HIGH ELEVATION FOREST AVIAN COMMUNITY IN NORTHEASTERN NORTH AMERICA

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Montane forests provide habitat for unique assemblages of flora and fauna that contribute significantly to a region's biodiversity. Previous work indicates that montane forest ecosystems are exceedingly vulnerable to a host of anthropogenic stressors including climate change, atmospheric deposition, and recreation, to name a few. Montane forests and other high elevation ecosystems are considered to be among the first and most severely impacted by climate change. It is therefore, imperative to evaluate anthropogenic impacts on montane ecosystems and maintain reliable monitoring methods that are capable of tracking potential shifts in the distribution of species dependent on these systems. I surveyed birds at various distances from hiking trails in the White Mountain National Forest from 2006 - 2009 to determine whether existing monitoring programs, all of which are based on trail-centered surveys, are accurately reflecting bird abundance, abundance stability and recruitment. Contrary to previous studies, I found that recreational trails generally did not alter estimates of abundance, recruitment,

abundance stability, and detection probability for five species of birds considered to be indicators of montane forest ecosystem integrity in northeastern North America. Therefore, trail-based monitoring programs for montane birds appear to accurately reflect dynamics of bird communities undisturbed by hiking trails. These conclusions were supported by my finding that the daily nest survival of a montane spruce-fir indicator species, blackpoll warbler (*Steophaga striata*), did not vary as a function of distance from trail.

I then used data from the White Mountain National Forest's montane bird monitoring program from 1994 through 2009 to assess potential shifts in the elevational distribution of montane birds in conjunction with documented habitat shifts in the region. My results provide evidence that low elevation forest birds have expanded their upper elevational boundary while high elevation birds have expanded their lower elevation boundary. These results highlight the complicated relationship between habitat, climate, and other anthropogenic stressors such as atmospheric deposition and that even in the face of climate change other stressors may be playing a significant role in shifts of species distributions.

Understanding how climate affects the reproductive ecology of montane organisms is an important step toward unraveling the potential mechanisms by which climate change will alter the distribution of these species. I used blackpoll warbler breeding data from the Green Mountains, VT from 1994 to 2003 to determine if temporal variation in climate influenced blackpoll nesting initiation and found that years with warm Mays and typical precipitation lead to earlier nest initiation. I also examined the

effect of spatial variation in climate on blackpoll reproductive ecology and demography. I found a gradient in habitat quality associated with the spatial variation in climate along an elevation gradient. Blackpolls were less abundant, younger, had lower pairing success, lower daily nest survival, higher nest predator occupancy, and lower fecundity at lower elevations. The climatic conditions at these lower elevations represent the climatic conditions predicted to encompass increasingly larger portions of montane areas. Collectively, these findings contribute to filling in a dearth of knowledge regarding management and an understanding of how species dependent on montane ecosystems are responding to climate change.

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CHAPTER 1

EFFECTS OF RECREATIONAL HIKING ON HIGH ELEVATION BIRDS

1.1 Introduction

High elevation forests provide habitat to a diverse and unique avian community. Current research suggests that montane ecosystems are susceptible to a host of stressors, including atmospheric deposition (Rimmer et al. 2005), and climate change (Rodenhouse et al. 2008). Montane bird communities of the northern Appalachian Mountains may be particularly vulnerable to these stressors due to their close proximity to dense human population centers. King et al. (2008) found population declines between 1993 and 2003 in the White Mountains, NH for three montane bird species, two of which, yellow-bellied flycatcher (see Appendix A for scientific names of birds) and Bicknell's Thrush, are considered ecological indicator species for montane spruce-fir forests. These findings not only emphasize the need to identify specific anthropogenic stressors that may be causing declines in mountain bird populations, but also highlight the importance of accurate monitoring programs that are essential for detecting and tracking such declines.

Currently, the Breeding Bird Survey (BBS) is the primary program for monitoring populations of North American birds (Sauer and Link 2011); however, this program notoriously underrepresents habitats that are relatively rare across the landscape (Bart and Peterjohn 1995, Thogmartin et al. 2006). In New Hampshire, montane spruce-fir forests encompass approximately 2% of the landscape (Lambert et al. 2005), most of which is inaccessible by roads and is therefore unavailable for sampling by the BBS. Because the vulnerable montane bird community of the Northeast is, therefore relatively unmonitored,

two long-term monitoring efforts have been implemented in the region. One monitoring program developed by the White Mountain National Forest began in 1993 and uses 42 routes established on hiking trails to sample most montane spruce-fir habitat patches within the forest (King et al. 2008). The other program, Mountain Birdwatch was established in 2000 and uses 96 routes along recreational hiking trails throughout New York, Vermont, New Hampshire, and Maine (Scarl 2011). Although these survey programs focus on important ecosystems, they are potentially hampered by their restriction to hiking trails, warranting similar scrutiny as the BBS for being limited to roads (Thogmartin et al. 2006). The location of survey points along roads or trails raises two important issues. The first issue is whether or not the potentially unique habitat and disturbance level of road and trail-based locations alters a surveyor's ability to detect birds. The second issue is whether bird communities sampled along roads and trails are accurate representations of communities not located along roads (Thogmartin et al. 2006). Although disturbances along trails are considerably less than those along roads, the same potential shortcomings attributed to the BBS roadside survey protocol may apply to trail-based surveys. Despite the fact that all montane bird monitoring programs in northeastern North America are dependent on trail-based surveys, there is little understanding of how accurately they might represent the montane bird community as a whole (Lambert et al. 2008).

Although recreational hiking trails offer efficient access to remote locations within montane habitats, evidence exists that suggests the abundance of some species is lower near trails compared to locations further from trails. Heil et al. (2007) found that recreational trails influenced montane birds of Argentina at three different levels:

community, guild, and population. At the community level, transects located on recreational trails resulted in lower bird species richness and diversity. At the guild level, the relative density of insectivorous species was reduced along trails and at the population level, lower densities were recorded along trails for six of the 28 species considered. Furthermore, human intrusions have also been shown to reduce the abundance of some montane species in western North America by 46-57% (Gutzwiller and Anderson 1999). Findings such as these, call into question whether trail-based surveys are representative of locations away from trails.

The effect of hiking trails on birds has implications for the validity of trail-based surveys, and can therefore have consequences for the conservation and management of this vulnerable bird community. Most montane forests of the northern Appalachians are protected as wilderness areas and are managed for wildlife and recreation (King et al. 2008). Recreation in these areas is primarily comprised of non-motorized, heavily used hiking trails. Although such recreational activities are believed to be low-impact, persistent human intrusions have been shown to have negative effects on wildlife, particularly birds (Knight and Cole 1995). Human intrusions similar to those found on recreational hiking trails have been shown to alter the timing of singing for several montane species (Gutzwiller et al. 1997). Low levels of human intrusions have also been shown to reduce singing rates of some montane species (Gutzwiller et al. 1994). Singing is an important part of the reproductive ecology for many forest passerines. A male's primary song is most importantly used to attract females (Eriksson and Wallin 1986) and to establish and defend territories (Krebs et al. 1978). Furthermore, human intrusions into a bird's territory may ultimately have a significant negative affect on reproductive

success by altering the frequency and timing of male singing. Human intrusions have also been found to directly influence the reproductive success of some birds. Miller et al. (1998) found that some species avoid nesting near trails and that nest survival increased with increasing distance from trails in grassland and forest habitats. It is reasonable to consider recreational hiking as a potential stressor contributing to population declines found by King et al. (2008) and Lambert et al. (2008), particularly since approximately five million visitors use the White Mountain National Forest annually.

Although trail-based recreation has been shown to negatively affect abundance and breeding ecology of montane birds elsewhere in North and South America, which could invalidate trail-based surveys and negatively affect populations, there have been no detailed studies of the effect of recreational trails on detectability, reproductive success and demography of montane birds in eastern North America. I surveyed birds to derive estimates of detection probability, abundance, abundance stability, and recruitment to test several hypotheses. I tested whether mountain bird abundance is lower at on-trail survey locations than at interior forest locations. Next, I tested whether detection probabilities vary between surveys located on the trail and surveys located at various distances from the trail. I then tested whether abundance stability and recruitment rates within and among breeding seasons vary with distance to trail. In addition, I used a montane spruce-fir obligate, blackpoll warbler to test whether distance to recreational hiking trails influence daily nest survival.

1.2 Methods

1.2.1 Study area and site selection

Surveys were conducted in 2006 and 2007 at 10 sites within the Presidential Range and Crawford Notch region of the White Mountain National Forest (N44°7' to N44°21' W71°27' to W71°14'), encompassing approximately 46,000 ha. Each site encompassed a segment of hiking trail classified by the White Mountain National Forest as having heavy volume of hiking traffic. One of the trails selected for surveys, Caps Ridge Trail on Mount Jefferson of the Presidential Range, was also selected as a site to monitor blackpoll warbler daily nest survival from 2006 to 2009.

Four survey locations were established on each trail with distances between survey locations no less than 250 m and no more than 1 km. Survey locations were spaced evenly along hiking trails at a site so that the most complete elevational gradient was surveyed, typically between elevations of 750 m above sea level (asl) and approximately 1500 m asl (treeline). Within this elevation zone, the vegetation is characterized by a transition from a high canopy, mixed coniferous-deciduous forest to a low canopy forest dominated by balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) with inclusions of paper birch (*Betula cordifolia*) and mountain ash (*Sorbus americana*; Sabo 1980). Two other survey locations were established for each survey on the trail; one at 200 m and one at 400 m perpendicular to the trail. Ninety survey locations were surveyed in 2006; 40 survey locations were located on trails, 40 were located 200 m from a trail, and 10 were located 400 m from a trail. One hundred and thirteen survey locations were surveyed in 2007; 40 survey locations were located on

trails, 40 were located 200 m from a trail, and 33 were located 400 m from a trail. Survey locations were identical in 2007 as in 2006 with the addition of 23 new survey locations 400 m from the trail.

1.2.2. Field methods

Point count surveys in both years were conducted three times at each location during the height of the breeding season between 6 June and 17 July by one of four trained observers. Each survey consisted of a 10-minute point count during which all birds seen or heard were recorded as being either within 50 m of the survey location or >50 m of the survey location. Only singing males within 50 m were used for analysis. Surveys began at dawn and continued until 1100 hours. The first round of surveys within each year started at lower elevation sites and proceeded upslope, the second survey began at the highest elevations and proceeded downslope, and the last survey of the year followed the order of the first. Weather was given a score of one through four for each survey, where a score of one indicated clear conditions and a score of four indicated clouds with some drizzle. Wind was also given a score of one through four, where a one indicated calm conditions and a score of four indicated that wind was strong enough to move tree branches, but not the main trunk of the tree. Surveys were not conducted if weather or wind conditions warranted a score higher than four.

Habitat characteristics exhibited substantial variation among survey locations caused by larger scale influences, such as those driven by climate along the elevation gradient (Seidel et al. 2009) as well as smaller scale disturbances such as those driven by wind, ice, and exposure (Sprugel and Bormann 1981). Therefore, several habitat

characteristics were measured at each survey location. Twenty-five m radius subplots were centered on each survey location. Canopy height, canopy closure, mid-canopy height, and mid canopy closure were quantified within the subplot. Canopy and mid-canopy closure was visually estimated after calibration among observers. In addition, percent species composition was visually estimated within the 25 m subplot for the canopy and mid-canopy. A 10 m subplot was also established at the center of the survey location where all softwood (primarily balsam fir and red spruce) stems were counted and identified as being greater than or less than 10 cm diameter at breast height (DBH; Eliason 1986). The measured habitat characteristics were considered a parsimonious description of relevant habitat structure and composition.

Daily trail use was measured at each trail upon which surveys were conducted with a TrailMaster TM1000 active infrared trail counter. Daily trail use was collected for five to eight day periods, three times in 2007. The first trail use sampling period was between 7 June and 19 June, the second sampling period was between 23 June and 8 July, and the final sampling period was between 13 July and 24 July. Elevation was measured using a global positioning system.

Blackpoll nests were located by systematic searches of suitable vegetation as well as by following individuals displaying nesting behavior (e.g., carrying nest material or food). Nests were monitored every third day and nest success was determined following the recommendations of Manolis et al. (2000). Upon nest completion, I attempted to confirm success by searching for fledglings near the nest or being fed by a known parent because nest fate cannot be reliably assigned by nest condition (King and DeGraaf 2006). After a nest fledged, I recorded the elevation of the nest, diameter at breast height (DBH)

of the nest tree, height of the tree the nest was located in, and the shortest linear distance of the nest to the hiking trail. I also recorded slope, canopy height, canopy closure, % of canopy that was balsam fir, the number of balsam fir stems <10 cm DBH, and the number of balsam fir stems >10 cm DBH on a 10 m radius plot centered on the nest. Nest site variables were selected based on findings of Eliason (1986) and Dalley et al. (2009).

1.2.3 Data analysis

I used a multivariate analysis of variance (MANOVA) to determine whether habitat characteristics differed between trail, 200 m and 400 m survey locations. The dependent variables considered in the MANOVA are listed in Table 1.1. A Tukey's hsd test was then implemented for significant variables from the MANOVA to determine which distance-from-trail categories differed from each other. The MANOVA model was fit using the *manova* function in R, version 2.10.1 (R Development Core Team 2010). To determine if hiker activity on the sampled trails increased between the three sampling periods as the breeding season progressed, I used an analysis of variance (ANOVA) followed by a Tukey's hsd test to determine which sampling periods differed from each other. The ANOVA model was fit using the *aov* function and the Tukey's test was implemented with the *TukeyHSD* function in R.

I constructed a parsimonious set of habitat characteristic variables from the total set of 15 habitat variables (Table 1.1) with a Principal Components Analysis (PCA) that explained the variation in 15 habitat variables by extracting the dominant underlying environmental gradients (McGarigal et al. 2000). To assess the significance of each principal component I performed a Monte Carlo test with 1,000 permutations to test whether the observed eigenvalue was significantly different from the distribution of

eigenvalues under the null hypothesis. I used the eigenvectors and biplots to interpret the ecological meaning of principal components that were deemed significant at the $P < 0.05$ level. The reduced set of habitat variables were then used as independent variables in subsequent analyses. The principal component analysis was conducted using the *prcomp* function and the Monte Carlo permutation was conducted with the *ordi.monte* function in the BIOSTATS package (McGarigal 2011) in R-2.14.0 (R Development Core Team 2010). I then used ANOVA to test whether significant principal components varied by distance to trail, followed by a Tukey's HSD test to determine which distance-from-trail categories the principal components differed.

I used the Dail-Madsen model (Dail and Madsen 2011) to derive estimates of abundance (λ), recruitment (γ), abundance stability (ω), and detection probability (p) from point count data. Models were restricted to the 5 species of high elevation forest specialist birds with >40 detections. I compared parameter estimates between survey locations located on hiking trails, 200 m from hiking trails, and 400 m from hiking trails. The Dail-Madsen model is a generalization of the *N*-mixture model (Royle 2004) and allows for open populations between sampling locations and intervals while accounting for imperfect detection probability (Dail and Madsen 2011). The model is unique because it does not rely upon the assumption that survey locations are closed to population changes between locations and survey intervals and thus allows abundance to fluctuate over time. The Dail-Madsen model is also unique because it provides estimates of recruitment (γ) and abundance stability (ω) within a breeding season and among breeding seasons while incorporating covariates for both estimates for unmarked populations. I interpreted within and among breeding season estimates of ω as a measure of abundance

stability, defined as changes in abundance due to the loss of individuals to permanent emigration out of the survey area and/or losses due to mortality (Chandler and King 2011), such that estimates close to 1.0 were interpreted as minimal changes in abundance and estimates close to 0.0 were interpreted as substantial decreases in abundance. Recruitment and abundance stability were estimated at monthly intervals and then extrapolated for within and among breeding season estimates. This feature of the model was particularly valuable for this analysis because it enabled me to test whether or not birds responded by moving from trails by examining estimates of recruitment and abundance stability at the three distance-from-trail categories within and among breeding seasons.

I considered eight potential covariates for p including: wind, weather, temperature, observer, date, time, distance from trail, and elevation. I also reduced the effects of detection cue and distance on detection probability by limiting the analysis to only singing males within 50 m of the survey location (Chandler et al. 2009b). Distance-from-trail was used as a predictor for λ, γ, and ω in all models. Scores from significant principal components of habitat variables that varied with distance-from-trail were considered as covariates on all parameter estimates to control for the potentially confounding effects of habitat. Because many species have been shown to reach a maximum abundance at optimum elevation or habitat conditions (Able and Noon 1976), after which abundance can decline; I also considered quadratic polynomial terms for elevation and the habitat principal components. A season covariate for γ and ω was included in all candidate models to acquire estimates within and among breeding seasons. The model uses a binomial distribution to model ω and p and a Poisson distribution to

model λ and γ. The model requires that a value K be set large enough to account for the largest observed count (Dail and Madsen 2011). Values of K were set at 10 for each species except for the two most common species, blackpoll warbler and Swanson's thrush, which were set at 15. Dail-Madsen models were fit using the *pcountOpen* function from the "unmarked" library in R.

I compared models using AIC_c such that all combinations of candidate models were considered for covariates that performed better than the null model when compared univariately. I first assessed the effect of distance to trail on λ, γ, ω, and p by determining if the distance from trail variable was included in a supported ($\Delta AIC_c \leq 2$) model (Burnham and Anderson 2002). I then used a likelihood ratio test to compare the model with most support to the same including the distance-from-trail covariate. This comparison was conducted independently for λ, γ, ω, and p for each species to identify which parameters were responsible for increased model performance. Finally, parameter estimates for λ, within breeding season γ, among breeding seasons γ, within breeding season ω, among breeding seasons ω, and p were generated for survey locations on the trail, 200 m and at 400 m from the trail by including the distance-from-trail covariate in the model with most support for each species. I compared the 95% confidence intervals of the parameter estimates for survey locations on the trail, at 200 m from the trail and at 400 m from the trail for each species. If confidence intervals overlapped, it was considered further evidence that the parameter was not affected by distance-from-trail.

I used the logistic-exposure model described by Shaffer (2004) to determine whether distance from trail affects daily nest survival. The logistic-exposure model is a generalized linear model with a binomial error distribution and a modified link function:

$g(\theta) = \ln [\theta^{1/t}(1 - \theta^{1/t})]$, where θ is the nest survival estimate and t is the observation interval in days. To calculate exposure days I used the midpoint between the final two nest checks for unsuccessful nests (Manolis et al. 2000). I compared candidate models with a forward selection process considering all nest site variables using AIC_c and assessed the effect of distance to trail on daily nest survival by determining if the distance from trail variable was included in a supported ($\Delta AIC_c \leq 2$) model (Burnham and Anderson 2002). I then performed a likelihood ratio test between the model with most support (null model) and that same model with the distance from trail variable. Regression models were fit using the *glm* function in the R package "glm".

1.3 Results

Habitat characteristics differed among the three distance-from-trail categories ($F_{2, 110} = 1.95$, $P = 0.003$). This difference appears to be driven primarily by percent balsam fir in the canopy and mid-canopy height, as they were the only two significant univariate comparisons ($P = 0.02$ and $P < 0.001$, respectively). Percent balsam fir in the canopy was greater at sites 200 m from the trail compared to 400 m from the trail ($P = 0.02$; Table 1.1). Mid-canopy height was greater at sites 400 m from trails compared to on-trail sites ($P < 0.001$) and sites 200 m from trails ($P < 0.001$; Table 1.1).

Dominant gradients of habitat variation were represented by three principal components that explained 46% of variation in the data. The first principal component described sites along the elevation gradient varying in structure, with decreases in canopy height and mid-canopy height, and increases in small softwood stem densities (Figure 1.2). The second principal component primarily described variation in forest

composition from sites with abundant, large balsam fir trees in the canopy with a fir dominated mid-canopy to sites dominated by red spruce (Figure 1.2). The third principal component described variation associated with smaller scale disturbances resulting in localized regeneration. These sites were characterized by open canopies, abundant standing dead trees with relatively abundant regeneration (Figure 1.2). Principal component 1 showed some evidence of varying with distance from trail ($F_{2, 110} = 15.57$, $P = 0.06$). There was some evidence that principal component 1 differed between survey locations on trails and 400 m from trails ($P = 0.09$) as well as between survey locations 200m and 400m from the trail ($P = 0.10$), but not between survey locations on trails and 200 m from the trail ($P = 0.76$). Principal component 2 was significantly different between the distance-from-trail survey locations ($F_{2, 110} = 15.28$, $P = 0.03$). Principal component 2 did not differ between trail survey locations and locations 200m ($P = 0.73$) or 400m ($P = 0.13$) from the trail, although principal component 2 did vary between sites 200m and 400m from the trail ($P = 0.02$). Therefore, both principal component 1 and principal component 2 were used as covariates in subsequent Dail-Madsen models.

Mean daily trail hiking traffic of the first sampling period (6.5, SD = 5.8) was significantly lower than the second (57.9, SD = 55.4) and third (53.7, SD = 63.3) sampling periods ($P < 0.0001$ for both comparisons). Daily trail use between the second and third sampling periods were similar ($P = 0.87$).

I recorded 4,673 detections of 49 bird species during the study (Appendix A). Fifteen of these species are commonly found in high elevation spruce-fir forests in northeastern North America (Appendix A). The remainder of species also breeds in lower elevation mixed coniferous-deciduous forests (Poole 2008). Dail-Madsen models

explained 27-53% of the variation in high elevation bird abundance (Table 1.2). Distance-from-trail was not included as a covariate for λ, γ, ω, or p in any of the supported models for blackpoll warbler, Bicknell's thrush, Swainson's thrush, yellow-bellied flycatcher and boreal chickadee (Table 1.2). Likelihood ratio tests generally confirmed these results as the best models performed better without the distance-from-trail covariate for λ, γ, ω, or p for blackpoll warbler, Bicknell's thrush, Swainson's thrush and yellow-bellied flycatcher (Table 1.3). For boreal chickadee, the best models performed better without the distance-from-trail covariate for λ and p; however, models including distance-from-trail as a covariate for γ and ω differed from models that did not include distance-from-trail (Table 1.3). Parameter estimates for λ, within breeding season γ, among breeding seasons γ, within breeding season ω, among breeding seasons ω, and p did not vary as a function of distance-from-trail for any species (Table 1.4).

Thirty-five blackpoll nests were monitored on Mount Jefferson, 11 of which failed. Nest site characteristics varied widely (Table 1.5). There was no strong support for logistic-exposure models that included distance-from-trail (Table 1.6). The likelihood ratio test confirmed that a model containing the distance-from-trail covariate did not fit better than one without ($\chi^2 = 0.98$, df = 1, $P = 0.40$).

1.4 Discussion

I found little evidence that recreational hiking trials had adverse effects on high elevation bird abundance, detection probabilities, or demography in the White Mountains, NH. These findings suggest that trail-based surveys are a valid methodology for sampling montane birds in northeastern North America, and also that recreational

hiking is not likely to be contributing significantly to population declines of montane bird species. Although previous studies have examined the effects of recreational hiking on bird distribution and abundance (Miller et al. 1998, Gutzwiller and Anderson 1999, Heil et al. 2007, Cardoni et al. 2008, Kangas et al. 2010), reproductive ecology (Miller and Hobbs 2000, Gutzwiller et al. 2002b, Smith-Castro and Rodewald 2010), and behavior (Gutzwiller et al. 1997, 1998, Smith-Castro and Rodewald 2010), this study is the first to examine the influence of recreational trails on bird abundance and distribution while accounting for imperfect detection probabilities in a hierarchical framework. Furthermore, by implementing the Dail and Madsen model (2011), this study was the first to determine that recruitment and abundance stability was not affected by recreational trails both over the course of a breeding season and between breeding seasons.

It is important to directly account for imperfect detection probabilities when estimating abundance because detection probabilities can vary with relatively small differences in habitat (MacKenzie 2006a). Trail-side plant communities are often denser in structure than surrounding habitat due to increases in light penetration (Hall and Kuss 1989) or higher densities of invasive species (Lundgren et al. 2004, Davies and Sheley 2007). Habitat differences could lower detectability, which could be incorrectly interpreted as a decrease in abundance near trails. The effect of habitat on bird detections has been addressed to varying degrees in previous studies that found effects of either hiking trails or human intrusions on birds. However, none directly accounted for imperfect detection probabilities in their estimates of abundance or occupancy (Miller et al. 1998, Gutzwiller and Anderson 1999, Heil et al. 2007, Kangas et al. 2010). Heil et al.

(2007) limited the survey area to 30 m from the transect to minimize the effect of habitat on detecting birds, Gutzwiller and Anderson (1999) did not directly incorporate habitat in their estimates of abundance since they determined that habitat did not differ between control sites and sites with human intrusions, and Kangas et al. (2010) and Miller et al. (1998) did not account for the effect of habitat on detecting birds. If imperfect detection probabilities are not accounted for, it is difficult to rule out the possibility that differences between on and off trail sites in abundance or densities are not due to lower detectability rates in denser habitat near trails (Bibby 2000). I directly accounted for imperfect detection probabilities when estimating abundance by applying the generalized *N* mixture model developed by Dail and Madsen (2011).

It is unclear if the differences in the bird community found by the Miller et al. (1998) were driven directly by human intrusions or indirectly by birds responding to differences in altered plant communities near the trail. Other studies that found an effect of hiking traffic on bird communities controlled for the indirect effect of habitat differences (e.g. denser vegetation structure near the trail) by either confirming the that there were no habitat differences (Gutzwiller and Anderson 1999) or by including remotely sensed habitat characteristics as covariates in their models (Heil et al. 2007, Kangas et al. 2010). Although I found that mid-canopy height was lower at trail sites versus sites at 400 m, in general the plant community was similar between trail sites and sites at 200 and 400 m from the trail (Table 1.1). This is not unexpected because the trails in this study were in forests with relatively closed canopies, as indicated by the lack of differences in canopy closure between trail and off-trail survey locations. As a result, light penetration that could increase structural complexity near trails and thus, potentially

affect detectability, was likely not important in our study. Furthermore, by including the habitat principal components in the hierarchical models, habitat variation was controlled for when estimating parameters. Therefore, it appears that high elevation bird abundance is not directly influenced by hiker activity and because the trail-side plant community is relatively similar to the surrounding forest, there are no important variations in the plant community to drive differences in bird abundance.

This is the first study to examine the effects of recreational hiking on within and among breeding season movements in birds, potentially providing a refined measure of birds' response to disturbances. At my study sites, most birds arrive by late May, before hiker traffic reaches its peak, providing a "natural experiment" with before and after treatments with controls (locations 200 m and 400 m from trails). For blackpoll warbler, Bicknell's thrush, Swainson's thrush, and yellow-bellied flycatcher I found no evidence that individuals that establish territories near trails are likely to move from those locations either as the breeding season progresses or between breeding seasons. I also found that for the same species, sites at 200 and 400 m from the trail are no more likely to be settled than trail sites as the season progresses or between breeding seasons. Despite the fact that hiker activity dramatically increased over the course of the breeding season, it appears that for these species, whatever negative consequences are associated with repeated human intrusions, they were not sufficient enough to warrant abandoning a territory during the course of the breeding season. Kangas et al. (2010) found that occurrence and composition of bird communities were altered by recreational hiking in a protected area in Finland; however, hiking pressure in their study contributed much lower to model performance than measures of habitat characteristics. They questioned whether

the relatively low contribution of hiking pressure when explaining variation in bird occurrence was due to the fact that hiking visits are relatively low when birds are arriving and settling on territories in May and June compared to later in the season. By showing that abundance stability and recruitment did not differ over the course of a breeding season under similar changes in hiking pressure as documented in Kangas et al. (2010), my study suggests that variations in hiking traffic over the course of a season do not affect abundance or occurrence.

This study is the first use hierarchical models that explicitly estimate abundance stability and recruitment to examine the effect of hiking traffic on within and among season changes for birds. Most models that estimate occupancy or abundance while accounting for detection probabilities assume that survey locations are closed, meaning that new individuals do not enter or existing individuals do not leave survey locations between surveys over the course of a season (MacKenzie et al. 2003, Royle 2004). Dail and Madsen's model (2011) does not have this assumption and has the capability to derive estimates of recruitment and abundance stability between survey events. For Swainson's thrush, yellow-bellied flycatcher, and boreal chickadee, within season recruitment was practically zero and within season abundance stability was nearly one (Table 1.4). This indicates that, for these species, the survey area was closed to movements between surveys and the closure assumption for the MacKenzie (2003) and Royle (2004) models were met. Bicknell's thrush and blackpoll warbler, however, showed some evidence of movement into and out of the survey areas (Table 1.4), and would have violated the assumptions of the closed models. This finding is an important consideration for future studies applying the MacKenzie (2003) and Royle (2004b)

models and confirms that interpreting the results of these models as absolute abundance should be met with caution (Chandler et al. 2009b).

I did not find evidence that detection probabilities differed between trail sites and sites at 200 or 400 m, suggesting that changes in song consistency and/or song occurrence between trail and off-trail locations were similar. However, Gutzwiller et al. (1994) found that for some subalpine birds, song occurrence and consistency differed between sites experimentally exposed to human intrusions and control sites. Although I did not explicitly measure song consistency or occurrence, it is possible that some differences may exist as a function of distance-from-trail but the signal may not have been strong enough to be identified by a surrogate measure such as detection probability. Furthermore, surveys were conducted between dawn and 1100 hours, a majority of the surveys occurred before daily hiking activity peaked. It is possible that detection probabilities could have varied as a function of distance-from-trail if surveys were conducted during peak daily hiking activity. However, Gutzwiller et al. (1994) found an effect of song consistency and occurrence when experimental intrusions were applied between one and six days prior to surveys. Based on my findings that detection probabilities of singing males was not related to distance-from-trail, it is unlikely that recreational hiking has a functional influence on the singing behavior for these species in high elevation forests of White Mountains, NH.

Although the majority of my results found no evidence of recreational hiking having an influence on montane birds, this conclusion should be met with caution for species such as the gray jay (*Perisoreus canadensis*), for which I had insufficient samples to analyze. Gray jays have been known to be attracted to supplemental food sources

provided by hikers (Gutzwiller et al. 2002a) which may result in higher abundance along hiking trials. Furthermore, the likelihood ratio test provided some evidence that, for boreal chickadee, abundance stability and recruitment may vary as a function of distance-from-trail. Parameter estimates indicate that these differences may be driven by among breeding season movements as recruitment and abundance stability are higher, although not significantly, at 200 and 400 m sites compared to trail sites (Table 1.4). It is possible that these differences are real and our sample sizes were too small given the variation in the data to detect significance. This could imply that boreal chickadee territories near trails are less reproductively successful causing individuals to selectively move from these sites between breeding seasons.

Daily nest survival was not influenced by the distance of the nest to the trail. Previous studies have found conflicting results. Miller (1998) found that nest survival increased with increasing distance from trails, while Miller and Hobbs (2000) found that nest predation rates were higher further from trails. The assumption is that mammalian and avian nest predators are more abundant and have greater access to nests near habitat edges or corridors because predators frequently travel along habitat edges or established routes (Hickman 1990, Rich et al. 1994). Red squirrel (*Tamiasciurus hudsonicus*) is one of the primary mammalian nest predators of birds in the montane forests of the White Mountains, NH (Holmes 2011). Within the relatively unfragmented landscape of the White Mountains, it is possible that small corridors, such as recreational trails, are not disproportionately frequented by red squirrels because habitat near trails does not differ from habitat further from trails (Table 1.1) in a way that facilitates travel.

My finding that nest survival rates did not vary as a function of distance from trail is consistent with my observation that abundance, recruitment, and abundance stability also did not vary with distance from trail. This implies that not only was bird abundance near trails similar to sites further from trails, but that breeding success near trails was similar to areas further from trails. Because nest predation rates can vary with nest height (Sloan et al. 1998), these results might only be relevant to species that generally nest in a similar vegetation strata to that of the blackpoll warbler. Furthermore, forest passerines are typically more likely to have higher annual return rates to territories where they were reproductively successful during past breeding attempts (Hoover 2003). Therefore, my findings that these species were not more likely to move away from trails between breeding seasons may be an additional indication that relative breeding success does not substantially vary between trail and off-trail sites for other species for which we did not collect nesting data.

It is likely that abundance estimates from trail-based monitoring programs are reflective of abundance throughout the spruce-fir forest because I did not find abundance or detection probabilities to differ between trail and off-trail sites. These results imply that monitoring programs using trail-based surveys can be interpreted as valid representations for montane forest habitats in northeastern North America. The use of hiking trails in montane bird monitoring programs provides the efficiency of moving swiftly between surveys while avoiding the potentially compromising effects of road-based surveys that are biased to habitats that are likely to occur near roads and detection rates could be reduced by road-related noise levels (Thogmartin et al. 2006).

Much of the high elevation spruce-fir forest of northeastern North America has extensive and dense recreational trail networks. Because of the high trail density and activity, potential for substantial trail-based effects were present given the patterns found in previously mentioned studies. This study is one of the first to examine the effect of hiking trails on the vulnerable avian populations that inhabit these forests. Due to the remoteness of most of the high elevation habitat in the northern Appalachians, many of the typical anthropogenic stressors reported to affect avian populations of low elevation habitats such as habitat loss, fragmentation, and isolation, are not relevant in this study. Recreational hiking trails are therefore believed to be one of the few direct anthropogenic influences on these populations. Based on the results of this study, it is not likely that hiking trails are playing a significant role in the declines in montane birds reported by King et al. (2008). Future research should look towards the assessing atmospheric deposition, climate change, and habitat alteration during the nonbreeding season as potential sources for these declines.

Table 1.1: Summary statistics (mean ± SD) for habitat variables measured at 113 survey plots in the White Mountain National Forest in 2006 and 2007. Superscripts indicate significant differences between distances from trail for % canopy balsam fir and mid-canopy height. Significance was determined by Tukey's hsd test at $\alpha = 0.05$.

Variable	Abbreviation	Trail	200 m	400 m
Elevation	elev	1060.2 ± 172.0	1068.7 ± 159.5	1037.3 ± 143.7
Canopy height (m)	canH	10.3 ± 4.5	11.2 ± 5.1	12.1 ± 3.9
Canopy closure	canC	64.6 ± 20.6	66.5 ± 14.1	64.6 ± 18.4
% canopy balsam fir	canFir	53.8 ± 25.4^{ab}	61.4 ± 26.0^{a}	44.9 ± 23.3^{b}
% canopy red spruce	canSpr	12.1 ± 20.9	15.4 ± 23.0	21.8 ± 19.2
% canopy paper birch	canBir	23.8 ± 19.7	20.0 ± 16.0	25.9 ± 18.9
% canopy mountain ash	canAsh	3.4 ± 6.7	1.0 ± 2.6	2.6 ± 4.9
% standing dead	snag	1.2 ± 3.7	0.3 ± 1.1	0.9 ± 2.3
Mid-canopy height (m)	midH	2.7 ± 1.9^{a}	2.9 ± 1.9^{a}	4.7 ± 2.0^{b}
Mid-canopy closure	midC	26.8 ± 25.2	33.0 ± 26.3	34.1 ± 16.8
% mid-canopy balsam fir	midFir	46.3 ± 35.4	57.3 ± 33.9	60.9 ± 24.1
% mid-canopy red spruce	midSpr	13.3 ± 20.9	12.8 ± 17.0	21.8 ± 16.4
% mid-canopy paper birch	midBir	6.0 ± 19.7	4.5 ± 8.7	8.6 ± 10.9
% mid-canopy mountain ash	midAsh	4.9 ± 8.1	5.1 ± 12.2	2.7 ± 5.5
# softwood stems > 10 cm DBH	softL	16.2 ± 17.4	19.7 ± 16.7	14.1 ± 11.6
# softwood stems < 10 cm DBH	softS	56.8 ± 38.7	58.6 ± 33.0	63.3 ± 40.6

Table 1.2: Results of Dail-Madsen model selection with $\Delta AIC_c < 2.0$. Covariates that influence abundance are listed in parentheses after λ, recruitment covariates are listed after γ, abundance stability covariates are listed after ω, and detection probability covariates are listed after *p* (E = elevation, H1 = principal component 1, H2 = principal component 2, D = date, O = observer, K = sky, W = wind, C = temperature, I = time). A season covariate for *γ* and *ω* was included in all candidate models to acquire estimates within and among breeding seasons. Squared terms indicate quadratic effects and a period indicates there were no covariate effects.

Species[a]	Model	*K*	ΔAIC_c	w_i	R^2
BLPW	λ(H1^2) γ(.) ω(.) *p*(O+W)	12	0.00	0.87	0.35
BITH	λ(H2) γ(H1) ω(H1) *p*(E+I)	11	0.00	0.14	0.34
	λ(H2) γ(H1) ω(H1) *p*(D+E+I)	12	0.08	0.13	0.36
	λ(H1+H2) γ(H1) ω(H1) *p*(D)	11	0.29	0.12	0.34
	λ(H1+H2) γ(H1) ω(H1) *p*(I)	11	1.69	0.06	0.35
BOCH	λ(H2) γ(H1^2) ω(H1^2) *p*(O+K)	15	0.00	0.22	0.33
	λ(H2) γ(H1^2) ω(H1^2) *p*(O+K+W)	16	0.66	0.16	0.33
	λ(H2) γ(H1^2) ω(H1^2) *p*(K+W)	13	0.75	0.15	0.30
	λ(.) γ(H1^2) ω(H1^2) *p*(O+K+W)	15	1.14	0.13	0.32
	λ(.) γ(H1^2) ω(H1^2) *p*(O+K)	14	1.18	0.12	0.31
SWTH	λ(.) γ(H1^2) ω(H1^2) *p*(C+W)	12	0.00	0.47	0.52
	λ(.) γ(H1^2) ω(H1^2) *p*(E+C+W)	13	1.02	0.28	0.53
YBFL	λ(H2) γ(.) ω(.) *p*(O+I+W)	12	0.00	0.40	0.31
	λ(.) γ(.) ω(.) *p*(O+I+W)	11	0.53	0.31	0.30
	λ(H1+ H2) γ(.) ω(.) *p*(O+I+W)	13	1.99	0.15	0.31

[a]BLPW=Blackpoll warbler, BITH=Bicknell's thrush, BOCH=Boreal chickadee, SWTH=Swainson's thrush, YBFL=Yellow-bellied flycatcher. See Appendix A for scientific names.

Table 1.3: Results of likelihood ratio test between best models and best including the distance-from-trail covariate for abundance, abundance stability and recruitment, and detection probability. Tests with significant differences are noted in bold. See Table 1.2 for species abbreviations.

Species	Abundance (λ)			Abundance stability (ω) and recruitment (γ)			Detection probability (*p*)		
	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
BLPW	0.39	1	0.82	4.74	2	0.32	3.15	1	0.21
BITH	4.58	1	0.10	0.63	2	0.73	2.47	1	0.29
YBFL	0.05	1	0.98	6.50	2	0.17	1.08	1	0.58
SWTH	3.42	1	0.18	0.15	2	0.87	4.62	1	0.10
BOCH	0.18	1	0.89	**10.56**	**2**	**0.03**	1.17	1	0.56

Table 1.4: Back-transformed parameter estimates ± 1 SE from the Dail-Madsen model with most support (see Table 1.2) with the distance-from-trail covariate. Coefficient SE's were back-transformed using the delta method (Powell 2007). 95% CI for each estimate overlapped between the three distance-from-trail categories for all species. See Table 1.2 for species abbreviations.

	Abundance (λ)			Recruitment (γ)						Abundance stability (ω)						Detection probability (p)		
				Within breeding season			Among breeding seasons			Within breeding season			Among breeding seasons					
Species	Trail	200m	400 m	Trail	200 m	400 m	Trail	200 m	400 m	Trail	200 m	400 m	Trail	200 m	400 m	Trail	200 m	400 m
BLPW	1.95± 0.30	1.75± 0.28	1.93± 0.31	0.08± 0.64	0.18± 0.85	0.06± 0.63	0.15± 0.14	0.23± 0.16	0.07± 0.11	0.98± 0.01	0.79± 0.12	0.92± 0.11	0.90± 0.01	0.89± 0.01	0.90± 0.01	0.98± 0.01	0.95± 0.004	0.97± 0.002
BITH	0.86± 0.29	0.57± 0.23	0.52± 0.18	0.04± 0.36	0.08± 0.28	0.06± 0.43	0.16± 0.14	0.13± 0.14	0.14± 0.14	0.71± 0.33	0.64± 0.29	0.69± 0.19	0.82± 0.09	0.79± 0.10	0.81± 0.10	0.22± 0.08	0.15± 0.08	0.09± 0.06
YBFL	1.02± 0.32	1.08± 0.33	1.02± 0.27	0.01± 0.01	0.01± 0.01	0.01± 0.01	0.21± 0.11	0.39± 0.13	0.33± 0.16	0.99± 0.01	0.99± 0.01	0.99± 0.01	0.61± 0.10	0.64± 0.10	0.63± 0.10	0.89± 0.11	0.89± 0.10	0.96± 0.07
SWTH	1.43± 0.23	0.95± 0.20	1.54± 0.27	0.01± 0.01	0.01± 0.01	0.01± 0.01	0.59± 0.15	0.67± 0.18	0.63± 0.17	0.99± 0.01	0.99± 0.01	0.99± 0.01	0.60± 0.10	0.54± 0.10	0.57± 0.10	0.96± 0.08	0.86± 0.15	0.91± 0.13
BOCH	0.73± 0.31	0.70± 0.28	0.69± 0.26	0.01± 0.01	0.01± 0.01	0.01± 0.01	0.16± 0.13	0.31± 0.15	0.36± 0.16	0.99± 0.01	0.99± 0.01	0.99± 0.01	0.49± 0.13	0.78± 0.11	0.83± 0.17	0.20± 0.08	0.17± 0.07	0.14± 0.07

Table 1.5: Summary statistics for blackpoll warbler nest site habitat variables measured at 35 nests on Mount Jefferson in the White Mountain National Forest from 2006 to 2008.

Variable	Mean ± SD	Range
Distance to hiking trail (m)	65.5 ± 45.7	3 – 192
Elevation (m)	1022 ± 44.5	939 - 1084
Slope (%)	8.5 ± 5.1	2 - 24
DBH of nest tree (cm)	10.2 ± 8.6	2.0 – 40.6
Canopy height (m)	10.1 ± 2.5	5 - 15
Nest tree height (m)	2.6 ± 1.7	0.8 - 8
% canopy closure	58.3 ± 19.2	20 - 85
% balsam fir in canopy	42.3 ± 19.8	10 ± 80
Small balsam fir stems*	102.3 ± 90.7	20 - 330
Large balsam fir stems*	7.2 ± 5.6	0 - 21

*Small stems < 10 cm DBH, large stems ≥ 10 cm DBH

Table 1.6: Parameter estimates of logistic exposure models of blackpoll warbler daily nest survival with $\Delta AIC_c \leq 2$. Estimates are in bold if 95% confidence intervals do not include zero. Covariates include % canopy closure (Can), diameter at breast height of nest tree (DBH), elevation of nest (Elev), and number of balsam fir stems <10 cm DBH (Fir). Vegetation variables were measured on a 10 m radius plot centered on the nest tree. Data are from 35 nests on Mount Jefferson in the White Mountain National Forest from 2006 to 2008.

β 0	Can	DBH	Elev	Fir	ΔAIC_c	w^a	R^2
-12.37		**0.38**	**0.41**	0.01	0.00	0.37	0.21
-14.01		**0.32**	**0.35**		0.36	0.35	0.19
0.84		**0.43**		0.01	1.86	0.17	0.17
-15.12	0.02	**0.15**	**0.35**	0.01	1.93	0.12	0.20

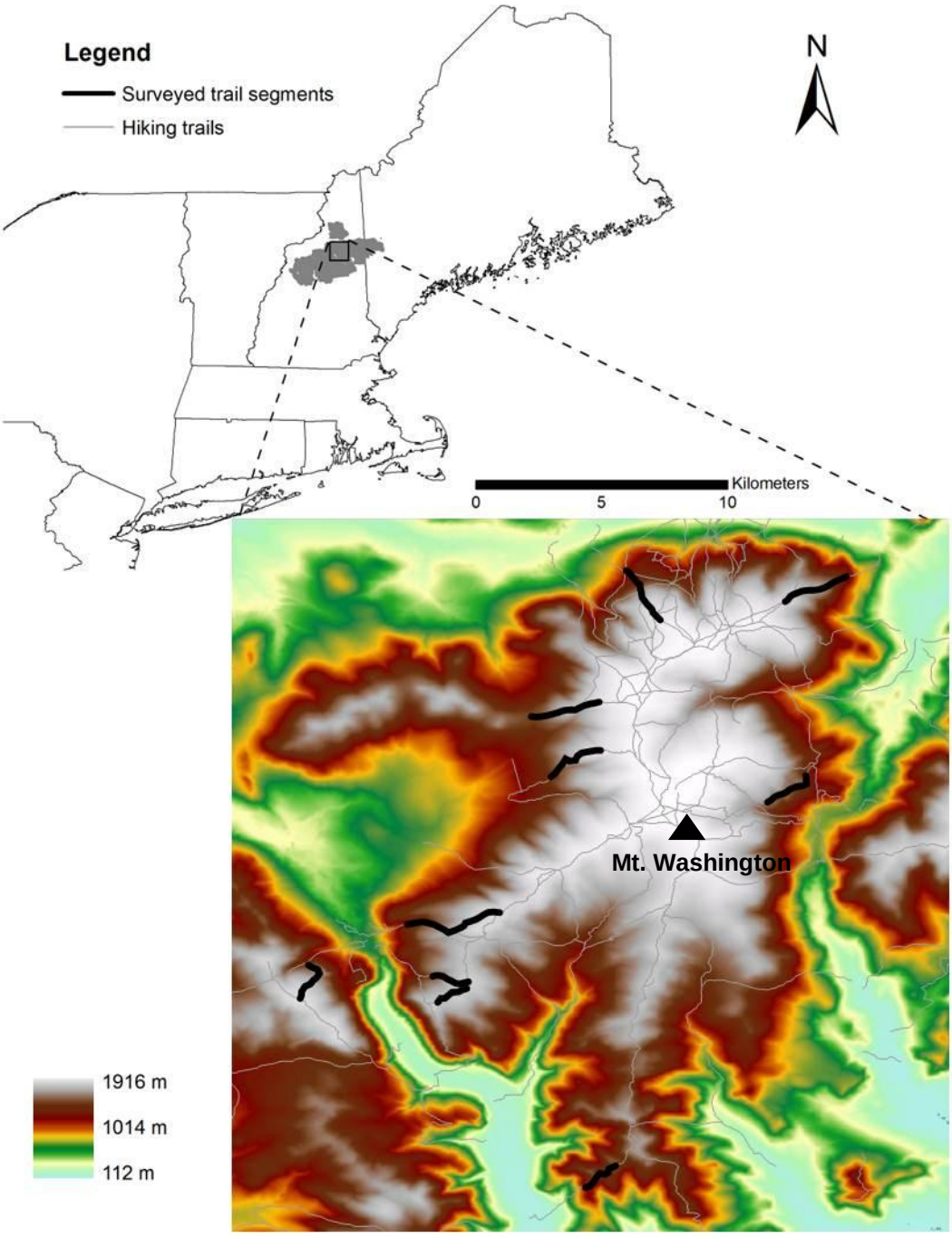

Figure 1.1: Digital elevation model of the study area within the White Mountian National Forest, NH, USA. Black lines indicate sections of trails that were survyed.

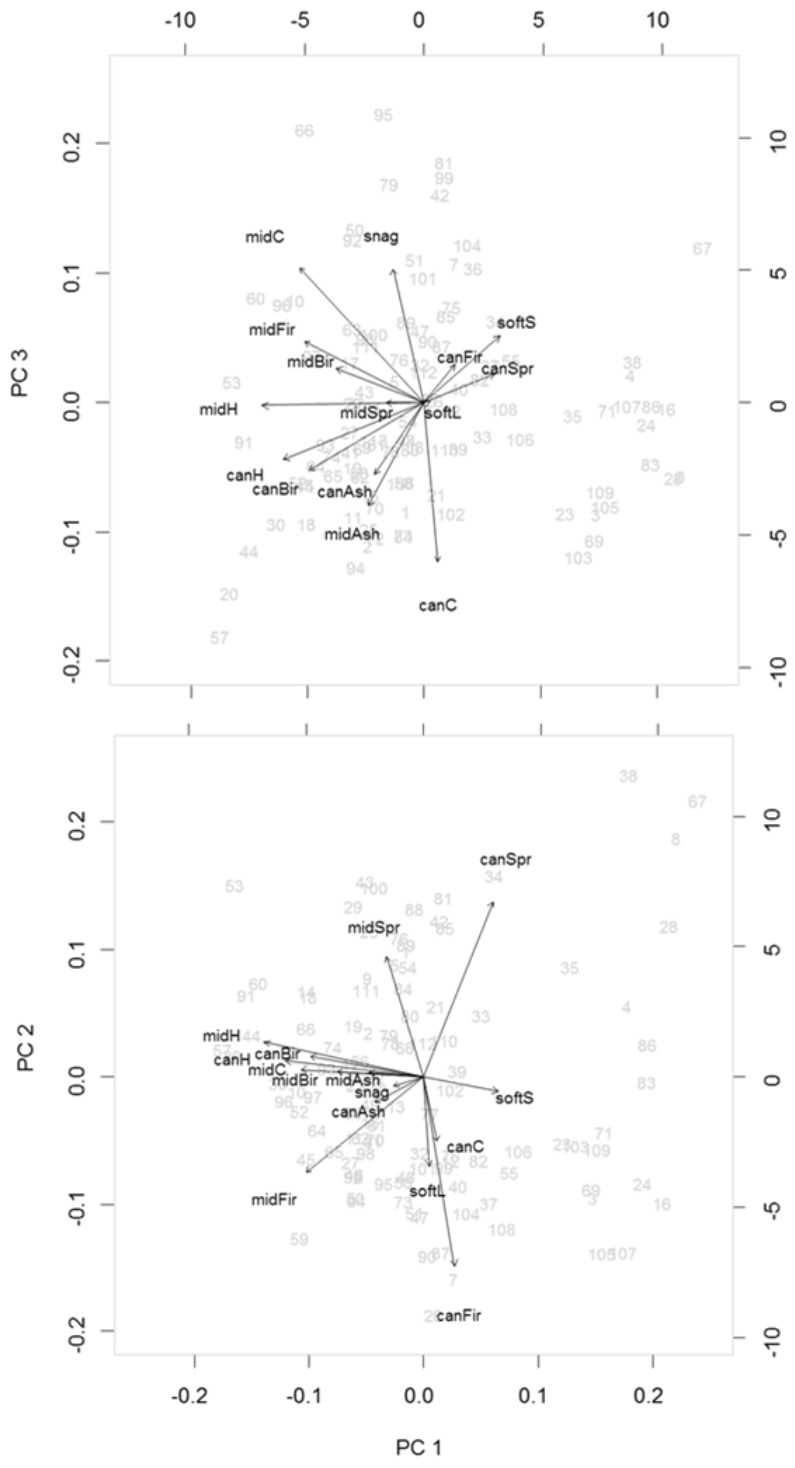

Figure 1.2: Biplots of a principal components analysis describing variation in habitat characteristics at 113 point count locations in the White Mountains, NH. Site scores are shown as numbers and the strength and direction of the habitat variables are shown as arrows. See Table 1.1 for variable abbreviations.

CHAPTER 2

RAPID SHIFTS OF MONTANE BIRD ELEVATIONAL RANGES: CLIMATE CHANGE AND OTHER POTENTIAL CAUSES

2.1 Introduction

Over the past 100 years, anthropogenic activities have changed the environment sufficient to alter the distribution of many species. The burning of fossil fuels, conversion of natural habitats for agricultural, commercial, or residential use, environmental contamination, and timber harvest are examples of activities that have altered the spatial distribution and composition of many habitats throughout the world (Solomon 2007, Pereira et al. 2008). Collectively, these anthropogenic stressors have contributed to one-fifth of extant vertebrates being classified as Threatened by the IUCN Red List, including 13% of all bird species (Hoffmann et al. 2010). Climate change in particular has been identified as a serious threat to the persistence of many species' populations (Root et al. 2003). To develop sound conservation strategies, it is imperative to increase our understanding of how of anthropogenic stressors influences the geographic distribution of species. This is particularly the case for high elevation species, which are not only believed to be exceptionally vulnerable to anthropogenic stressors such as climate change (Rodenhouse et al. 2008) and atmospheric deposition (Rimmer et al. 2005), but whose spatial distributions along an elevation gradient are driven by physiological constraints (Terborgh 1971), habitat requirements (Able and Noon 1976), and competition (Terborgh and Weske 1975).

Climate change is increasingly identified as one of the primary causes of recent species range shifts (Parmesan and Yohe 2003). Climate can lead to shifts in the geographic distribution of species in a number of ways. Morphological or physiological adaptations can constrain a species within a range of climatic conditions under which they evolved (Root 1988, Holt et al. 2005). Under this scenario, geographic shifts in climate (e.g., warmer temperatures shifting poleward), result in species shifts through their "tracking" of preferred or favorable conditions (Tingley et al. 2009, Zuckerberg et al. 2009). Alternatively, shifts in climatic conditions could affect bird species indirectly by altering habitat composition and structure (e.g., Beckage et al. 2008). Under this scenario, species shifts are the result of birds tracking changes in the spatial distribution of their preferred habitat conditions (Rodenhouse et al. 2008). For habitat specialists limited by specific habitat requirements, such alterations may result in geographic range contractions or complete extirpation (Sekercioglu et al. 2007). Finally, climate change can alter the distribution or abundance of invertebrates (Hodkinson 2005, Battisti et al. 2006). For insectivorous birds, a corresponding geographic shift may be necessary to acquire adequate energy (Visser et al. 2006).

Previous studies of bird communities along elevational gradients have increased our understanding of the mechanisms that drive species distributions (Terborgh 1971, 1985, Able and Noon 1976). Mountains offer opportunities for these studies because they typically have spatially compressed climatic zones, often ranging from warmer, drier climates at low elevations to cooler, wetter, and generally harsher climates at higher elevations, which typically correspond to compressed and distinct zones of vegetation communities that change dramatically over short distances with changes in elevation

(Able and Noon 1976, Reiners and Lang 1979, Sabo 1980, Terborgh 1985, Cogbill and White 1991).

More recently, studies along elevational or latitudinal gradients have been directed at documenting environmental changes due to climate change (Beckage et al. 2008, Seidel et al. 2009, Tingley et al. 2009). As the climate warms it is predicted that many climatic conditions typical of southerly latitudes and low elevations will shift away from the equator and increase in elevation (Solomon 2007). The vegetative composition and structure of ecological systems are predicted to be altered by the spatial shift of the climatic envelop encompassing favorable conditions of those systems (Parmesan and Yohe 2003, Sekercioglu et al. 2007, Sorte and III 2007, Zuckerberg et al. 2009). Beckage et al. (2008) has already found that the ecotone between northern hardwood forests and montane boreal forests shifted approximately 100 m upslope over the last 40 years in the Green Mountains of Vermont. Tingley et al. (2009) found that 91% of the bird species examined along an elevational gradient changed their geographic distribution to track their climatic (temperature and/or precipitation) niche between 1911-1929 and 2003-2008. Furthermore, Zuckerberg et al. (2009) documented a northward shift of 3.58 km in the mean latitude for 129 bird species sampled between 1980-1985 and 2000-2005 in the state of New York.

High elevation ecosystems, as with higher latitudes, are predicted to be particularly vulnerable to climate change (Rodenhouse et al. 2008). Abiotic factors such as climate play a stronger role in limiting species ranges in the harsher environments of higher latitudes and altitudes (Brown et al. 1996). Furthermore, the spatially compressed climatic and habitat zones of mountains restrict montane species ranges, leaving them

more susceptible to extirpation (Sekercioglu et al. 2007). The diversity of climatic conditions on mountains as well as the contrast of those conditions to the surrounding landscape typically result in montane areas contributing significantly to a region's overall biodiversity (Rahbek et al. 2007, Cadena et al. 2012). Consequently, mountains, particularly in the tropics, are regularly identified as global biodiversity hotspots (Rahbek 1997). Understanding how recent anthropogenic alterations of the environment are influencing the distribution of vulnerable montane species is an integral step towards their conservation.

Montane spruce-fir forest in the northern Appalachians supports a distinct avifauna (Able and Noon 1976), which includes species of high conservation concern such as the Bicknell's Thrush (*Cathurs bicknelli*; Lambert et al. 2008). Past research shows species characteristic of these vulnerable ecosystems have declined in recent decades (King et al. 2008, Lambert et al. 2008), and climate change is implicated as a potential cause of these declines. Recent evidence shows the climate in the northern Appalachians is changing (Beckage et al. 2008, Seidel et al. 2009).

In recognition of the vulnerability of montane ecosystems in general, as well as their proven value for investigating the effects of climate change, I used long-term bird survey data collected along an elevational gradient in the White Mountains, NH to assess whether changes in species elevational distributions have occurred since these surveys were initiated in 1992. Specifically, I tested for evidence of: 1) the upper elevational boundary of low elevation species shifting upslope; 2) the lower elevational boundary of high elevation species shifting upslope; 3) the center of occurrence of high elevation species shifting upslope; and 4) the upper elevational boundary of high elevation species

shifting upslope. I then put elevational range shifts in the context of population consequences by examining patterns in population growth to differentiate between actual range shifts and range expansions. Finally, I compare my findings for consistency with climate change predictions and offer alternative explanations for observed shifts.

2.2 Methods

2.2.1 Study area

This study was conducted in the White Mountain National Forest in northern New Hampshire (N43°53' to N44°32' W71°51' to W71°6') between the elevations of 740 m and 1470 m above sea level (asl). The White Mountain National Forest consists of an extensively forested area (>90%) encompassing 330,000 ha, 47,000 ha of which are designated as wilderness. Other areas of the forest are managed for timber harvest, recreation, and wildlife habitat (King et al. 2008). High elevation habitats are currently managed for recreation only.

The White Mountains provide suitable conditions for extensive montane boreal forests, with 30 peaks rising over 1300 m asl. Along the elevational gradient, forest community composition and structure changes rapidly. Below 750 m asl northern hardwood forests are dominant. Between 750 m asl and 1100 m asl, a mixture of deciduous and coniferous trees are present. With increasing elevation, coniferous species of the boreal forest become rapidly dominant. Above 1100 m asl the forest matrix consists of balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) with inclusions of paper birch (*Betula cordifolia*) and mountain ash (*Sorbus americana*) (Sabo 1980). Within this elevational range, forests are structured by frequent and widespread wind

disturbances (Sprugel 1976). From 1275 m asl to treeline the forest becomes dense with an associated decrease in canopy height, culminating in a Krumholz forest (Cogbill and White 1991). The climate in the White Mountains during the spring and summer is cool with high and variable winds. Orographic cooling causes increased precipitation with increasing elevation.

2.2.2 Field methods

Birds were surveyed by trained observers at fixed survey locations between 740 m and 1,470 m asl annually from 1993 to 2000, then in 2003, 2005, 2007, and 2009. Surveys consisted of 5 minute point counts, in which all birds seen or heard were recorded as being either less than or greater than 50 m from the observer. All surveys were conducted during the height of the breeding season (1 June to 25 June), under minimal wind and rain conditions between 0500 and 1100 EST. A total of 768 survey locations were surveyed on 42 separate transects located along hiking trails. Transects were established to provide broad coverage of nearly all the trails in the White Mountains within high elevation habitats. Individual survey locations were sampled 250 m apart along transects. Although the majority of points (approximately 70%) were sampled each year the survey was conducted, not all points were surveyed in all years primarily due to severe weather conditions. Elevation data for survey locations were recorded with a global positioning system (GPS). To acquire aspect and slope for survey locations, I used a 10 m digital elevation model in ArcGIS 9.3 geographical information system (GIS).

2.2.3 Statistical methods

Although a majority of locations were surveyed in all years, I examined the elevational distribution of surveys conducted each year to verify that the lack of sampling all survey locations every year did not bias the analysis. Because elevation range boundaries are unique for each species and could potentially lie anywhere within the range of elevations surveyed, I wanted to be confident there were no biases in the elevations of survey locations that were not conducted every year that could either mask or mimic potential species boundary shifts. To ensure this was not the case, I first inspected box and whisker plots of elevations of surveys conducted for every year. I then used linear regression models to determine whether the mean elevation of surveys changed over the 17 year period within every 100 m band from 740 m asl to 1470 m asl. I assessed survey elevations within every 100 m elevation band to confirm that there were no fine-scale, systematic biases in survey location elevations. Although the results presented here use all survey data, regardless of whether a point was surveyed in all years, separate anlyses were also conducted using only survey data from points that were conducted in every year for additional confirmation that subsequent findings were not an artifact of biased sampling (King et al. 2008). These procedures were conducted using R, version 2.10.1 (R Development Core Team 2010).

Only bird detections within 50 m of survey locations for species with >30 total occurrences were included in the analysis. Count data were transformed to presence or absence, and the binary data were then used to obtain an elevation for the occurrence of each species. This yielded elevations at which a species was present, which is henceforth termed its "elevational occurrence" for each species for each year.

Species detected during the study included those associated with lower elevations, for which survey points likely represented only the upper extent of their elevational distribution, as well as those considered high elevation forest obligates, which had elevational ranges that were encompassed within the elevational range of the surveys by design. To determine the extent to which a species' elevational distribution was captured within the elevation range of the surveys, I first calculated the proportion of points at which each species was present for every 25 m elevation bin between 740 m asl and 1470 m asl. A generalized linear model with a quadratic polynomial term for elevation was fit using the lm function in R for each species. The predicted values of a species proportional presence were then plotted against the elevational midpoint of each elevation bin. If it was apparent that the mode of the elevational distribution occurred below the survey elevation range then the species was considered to be a low elevation species, with a mode <750 m asl (e.g. Figure 2.2). Conversely, species whose elevational distribution mode fell within the elevation range of the surveys were considered high elevation species (e.g. Figure 2.2).

I used linear mixed-effects models to test for changes in species elevational occurrences between 1993 and 2009. I used a random intercept model with species elevational occurrence as the response variable, year as the predictor variable, and transect as the random effect. Mixed effects models were used to account for the non-independent errors of surveys spatially aggregated by transect (Zuur et al. 2009). Separate models were run for each species. Mixed models were implemented using the nlme package with the lme function developed by Pinheiro and Bates (2000). Spearman's rank correlation was used to determine that survey location slope and aspect

were highly correlated within transects (P=0.04 and P=0.03, respectively), two potentially important variables in determining species elevation distributions. Therefore, the transect variable also accounted for the potentially confounding effects of slope and aspect, enhancing the model's ability to test specifically for a change in elevation over time.

Since only the upper elevation distributions of low elevation species were captured within the elevation range of the survey, only the upper elevation boundary could be tested for elevation shifts over time for these species. I tested for elevation shifts in the sampled center of occurrence by applying the mixed effect model to the complete set of elevational occurrences for every low elevation species. To test for a shift in the extreme upper elevational boundary of low elevation species, I first selected the upper 90^{th} percentile of elevational occurrences for each year for each species, then I applied the mixed effects model only to elevational occurrences greater than the 90^{th} percentile. Because the distribution mode of elevational occurrences for low elevation species was not sampled, it is likely that the sampled center of occurrence and the sampled 90^{th} percentile represent a different portion of the upper boundary for each species. However, both measures are representations of the upper elevational boundary for low elevation species. Mixed models were also applied to the 60^{th}, 70^{th}, and 80^{th} percentiles of each species elevational distribution to retain the ability to examine general patterns because it is difficult to identify specific ecologically meaningful range boundaries.

For high elevation species, the majority of each species elevation distribution was sampled (e.g. Figure 2.2); therefore, I was able to test for shifts over time in the actual

lower elevational boundary, center of occurrence, and upper elevational boundary. Shifts in the lower elevational boundary were tested by selecting elevational occurrences within the 10^{th} percentile for each year, for each species and then implementing the mixed model. Mixed models were applied to all elevational occurrences for each species to test for shifts in the center of occurrence (mean of a species' elevation distribution). Changes in the upper elevational boundary were examined by applying mixed models to elevational occurrences within the 90^{th} percentile in each year for each species. Mixed models were also applied to every 10^{th} percentile of each high elevation species elevation distribution. The 90^{th} and 10^{th} percentiles were highlighted because they reflected elevational range extent and were not subject to the high variability that would be associated with the highest or lowest occurrence of each species, however because delineating a specific elevational "boundary" can be somewhat arbitrary (Maggini et al. 2011), I also applied these same mixed models to every 10^{th} percentile for comparison. Sample sizes for each model considered are reported in Appendix A.

I applied a nonparametric bootstrapping procedure to species' elevational occurrences using the boot function in the boot library in R to estimate the total change in elevation over the 17-year study period for the sampled center of occurrence and upper elevational boundary for low elevation species, and for the lower elevational boundary, center of occurrence, and upper elevational boundary for high elevation species. The data were sampled 10,000 times using the ordinary resampling method. For each sample the mixed model was applied to the data and the fixed effects estimates for the intercept and slope of the mixed model were inserted into the linear equation for 1993 and again for 2009 (this procedure provides an elevation estimate, in meters, for the specific portion

of the elevation distribution being considered). This enabled me to calculate the change in elevation for each species by subtracting the elevation estimate for 1993 from the elevation estimate for 2009. The statistical significance of observed shifts was assessed using 95% confidence intervals (CI) extracted from the 10,000 elevation change estimates by using the quanitle function in R to select the 0.025 and 0.975 quantiles. The bootstrapping procedure was applied to all high elevation species, but only to low elevation species that exhibited some evidence of a range shift (i.e. the fixed effect estimate of year differed from zero) during the original mixed modeling procedures for any of the distribution percentiles.

For all of measures of a species elevational distribution (lower elevational boundary, center of occurrence, and upper elevational boundary), I considered there to be evidence of a shift between 1993 and 2009 if the coefficient for the fixed effect of year on a species elevational occurrence (from the mixed models) was different from zero. The two measures of this difference I considered were that the 95% CI of the year estimate did not include zero and the *P* value for this estimate was < 0.05. For species for which bootstrapped estimates of elevation shift were calculated, additional support for elevation shifts was provided by the assessment of whether the 95% CI for the total change in elevation (m) between 1993 and 2009 included zero.

I used data from the North American Breeding Bird Survey (BBS) for New Hampshire (Sauer et al. 2008) to address the alternative hypothesis that range retractions (e.g., lower elevation boundary of high elevation species shifting upslope) were due to regional population declines and range expansions (e.g., upper elevational boundary of low elevation species shifting upslope) were due to regional population increases (Fuller

et al. 1995). For species exhibiting significant shifts in elevation with either the absence of significant (P<0.05) BBS trends or with significant trends opposite of what would be expected given the elevation shift (e.g., expanding boundary with population decline), I concluded the observed changes in the elevational boundary were due to an environmental response and not population fluctuations (Parmesan et al. 2005).

2.3 Results

Survey elevations did not change between 1993 and 2009 in any of the 100 m elevation bands between 700 m and 1500 m (Table 2.1). Therefore, all surveys were used in subsequent analysis. There were 75 species detected, 28 of which had sufficient sample sizes and were used for analysis (Appendix A). Of these 28 species, 16 were designated as low elevation species (elevation mode <750 m asl) and 12 as high elevation species (elevation mode ≥750 m asl; Table 2.2).

2.3.1 Low elevation species

Ten of the 16 low elevation species analyzed (62.5%) showed evidence of an elevation shift in their upper elevational boundary between 1993 and 2009 (Figure 2.3, Appendix B). Eighty percent of the low elevation species with support of an elevation change in their distribution shifted upslope over the course of the study. Black-capped chickadee (see Appendix B for scientific names) was one the only species that exhibited a downslope shift, which was evident in both its sampled center of occurrence and sampled upper elevational boundary (Figure 2.3). The sampled center of occurrence for black-

capped chickadee shifted -44.2 m downslope and its sampled upper elevational boundary shifted -154.1 m downslope from 1993 to 2009 (Table 2.2). Red-eyed vireo also exhibited a downward shift, but only at the 70th and 80th percentiles of its distribution (Appendix B).

Of the eight species exhibiting an upslope shift, the sampled center of occurrence shifted for 7 and the sampled upper elevational boundary shifted for three (Figure 2.3). Of the eight species with sampled center of occurrences that shifted upslope, five had 95% CIs, based on the bootstrapping procedure, that did not include zero (Table 2.2). For those five species, the average shift upslope was 125.2 m, with a range from 62.6 to 184.5 m (Table 2.2). The boostrapping procedure indicated that all three species with sampled upper elevational boundaries that shifted upslope had 95% CIs that did not include zero (Table 2.2). The average upward shift of the sampled upper elevational boundaries was 260.1 m (Table 2.2).

2.3.2 High elevation species

Nine of the 11 high elevation species analyzed (82%) showed evidence of a shift in either their center of occurrence, upper boundary or lower boundary between 1993 and 2009. However, only one species (11%), magnolia warbler, exhibited evidence of an upslope shift, while eight species (89%) showed some evidence of shifting downslope (Figure 2.4). Three species (27%) had upper elevational boundaries that underwent shifts between 1993 and 2009 (Figure 2.4). Magnolia warbler had an upper elevational boundary that shifted upslope and yellow-bellied flycatcher, white-throated sparrow and winter wren had significant downslope shifts of their upper elevational boundary (Figure

2.4). The bootstrapping technique provided further evidence that magnolia warbler's upper elevational boundary shifted upslope, increasing by 41.1 m over the 17-year period (Table 2.2). Two species, yellow-bellied flycatcher and winter wren, had upper elevational boundaries that shifted downslope by -22.1 m and -16.0 m, respectively. However, the 95% CI of the upper elevational boundary shift for these species did include zero (Table 2.2). Only winter wren had a significant shift of its center of occurrence (Figure 2.4), decreasing by -14.2 m from 1993 to 2009 (Table 2.2).

Six of the 11 (55%) high elevation species exhibited evidence of a shift in their lower elevational boundary (Figure 2.4). All six species had lower elevational boundaries that shifted downslope over the course of the study (Figure 2.4). Although a significant shift was not detected at the 10^{th} percentile measure of the lower elevational boundary for yellow-bellied flycatcher, the coefficient estimates were significant for the other measures of the lower elevational boundary (Appendix B). Further evidence of a downslope shift of the lower elevational boundary was provided by the bootstrapping technique for five of the six species (Table 2.2). Swainson's thrush, winter wren, Nashville warbler, yellow-rumped warbler, and dark-eyed junco had lower elevational boundaries that shifted downslope an average of -24.6 m (Table 2.2). Only blackpoll warbler had 95% CI that did not include zero (95% CI: -21.8 m to 0.0 m). In general, these patterns were consistent regardless of the percentile used to measure range boundaries (Appendix B).

2.3.3 Population trends

Of the 19 species that exhibited elevational range shifts in this study, six exhibited population changes according to BBS, and population trends could be a potential explanation of these shifts for only two species. The first was Swainson's thrush, which had an elevational range expansion and according to BBS has an increasing population and the second species was white-throated sparrow which has a decreasing population and exhibited evidence of elevational range shifts consistent with contraction (Figure 2.4). Thirteen species have populations that are stable. Three other species had decreasing populations, all of which exhibited evidence of elevational range expansions (black-and-white warbler, American redstart and Nashville warbler: Table 2.2). Although red-eyed vireo had some evidence of elevational range contraction, its population is increasing.

2.4 Discussion

My findings have provided evidence, that even in the face of a changing climate, shifts in species distributions can be highly unpredictable. Prevailing theory states that species distributions will move towards the poles and increase in elevation over time as a consequence of climate change (Parmesan and Yohe 2003, Brommer 2004, Parmesan et al. 2005, Parmesan 2006, Sekercioglu et al. 2007, Sorte and III 2007, Beckage et al. 2008, Rodenhouse et al. 2008, Zuckerberg et al. 2009). My findings support this idea for species typically found at lower elevations, as I provided evidence that most low elevation species have upper elevational boundaries that are shifting upslope from 1993 to 2009. However, most high elevation species, a group which is considered particularly

sensitive to climate change (Rodenhouse et al. 2008), shifted downslope over this period. Although other studies have documented species range shifts contrary to climate change predictions (Parmesan and Yohe 2003, Tingley et al. 2009, Zuckerberg et al. 2009), my findings that the majority of the bird community responded contrary to these predictions is unprecedented.

I found that within the White Mountains, two closely related bird communities are undergoing elevational range shifts in different directions. The mechanisms driving these opposing elevational shifts are potentially different for each bird community. There is evidence that temperature, potentially via physiological constraints, is a limiting factor defining the geographic range extent of many species (Grinnell 1914, Root 1988) including many of the low elevation species considered in this study (Venier et al. 1999). Temperature is thought to be an important determinant of elevational distributions of bird species along the compressed climatic zones of mountains in other regions of the world, such as the Andes (Terborgh 1971) and the Sierras of California (Tingley et al. 2009). Shifts in species distributions could thus, reasonably be associated with shifts in temperature. Data from Pinkham Notch, a site within my study area and at the approximate elevation of the hardwood forest-montane spruce-fir ecotone(612 m asl) indicates significant warming trends over the past 70 years (Seidel et al. 2009). Therefore, if low elevation birds are limited to lower elevations by cooler temperatures at higher elevations, then this rise in temperature at mid-elevations may allow them to shift their upper elevational boundaries upslope.

Climate-mediated changes in habitat are another potential mechanism by which climate change could affect the distribution of species. For example, Able and Noon

(1976) determined that most bird species inhabiting mountains in northeastern North America have distributional ranges that coincide with changes in ecotone. Elevational shifts in habitat consistent with those predicted from climate change were reported by Beckage et al. (2008), who found that the ecotone between the northern hardwoods and the montane forest has shifted upslope by approximately 100 m over the past 40 years. These upslope shifts in habitats characteristic of lower elevations and their associated resources could explain the upslope shift of the lower elevation bird species typical of northern hardwood forests observed in this study. This is supported by the similarity in the magnitude of the shift in ecotone reported by Beckage et al. (2008) and the average shift in elevation of low elevation species I observed (100 m and 125.2 m, respecitively). Although these elevational shifts are consistent with the view that shifts in elevational distribution is caused by shifts in habitat, it is not possible to determine with certainly whether or not the upslope shift of low elevation birds is driven directly by increasing temperatures or an upslope shift of suitable habitat because habitat and temperature shifts were coincident.

Changes in habitat and climate may also explain the down slope shift of the lower elevational boundary of high elevation birds. Although temperature may be the most important climatic factor limiting the distribution of some species, data from the Mount Washington Observatory (1914 m asl) did not indicate any significant change in temperature over the past 70 years (Seidel et al. 2009). However, other climatic variables such as precipitation may be particularly important for some species. Tingley et al. (2009) found that precipitation was the most important climatic variable when explaining the spatial distribution for many montane birds in the Sierra Nevada Mountains.

Furthermore, they found that precipitation was particularly influential to birds at intermediate elevations (726 – 1,107 m asl). This elevation range is similar to the transition zone in the White Mountains and comparable to the elevations into which the lower elevation boundary of high elevation birds are shifting. Precipitation has increased in northeastern North America over the past few decades (Huntington et al. 2009) and that increase is likely to be more pronounced at higher elevations (Howat et al. 2007), possibly due to increased cloud cover (Dai 2006) causing higher levels of orographic cooling. If precipitation is an important determinant of the distribution of high elevation birds in the White Mountains, as it is for many species in the Sierra Nevada Mountains, then some species may have to actually move down in elevation to track their precipitation climatic envelope. This may have particularly been the case for species like yellow-bellied flycatcher, winter wren and white-throated sparrow, whose upper elevational boundary and/or center of occurrence showed evidence of downslope shift.

While the increase of hardwoods in the ecotone between northern hardwood forests and montane spruce-fir (Beckage et al. 2008) may be enabling lower elevation birds to expand their ranges upslope, other compositional changes in the ecotone may also be allowing high elevation birds to expand their range downslope. Evidence suggests that red spruce is declining in northeastern North America and this decline is possibly caused by climatic change (McLaughlin et al. 1987, Johnson et al. 1988, Cook and Johnson 1989). However, orographic cooling-enhanced precipitation and cloud cover have led to higher levels of acidic deposition at higher elevations (Miller et al. 2005) and this is believed to be the most likely cause of spruce decline (McLaughlin et al. 1991, Joslin et al. 1992, McLaughlin and Kohut 1992, Lawrence et al. 1997, Shortle et al.

1997). One interesting result of this decline is the replacement of red spruce with balsam fir. Although overall hardwood basal area has increased within the transition zone, so too has balsam fir basal area due to the loss of red spruce (Battles et al. 1992, Beckage et al. 2008). All of the high elevation species I found to be shifting downslope are closely and specifically associated with balsam fir (Sabo and Whittaker 1979, Sabo 1980, Sabo and Holmes 1983). Therefore, the lower elevational boundary of some high elevation birds may be shifting downslope to track relatively recent increases in suitable habitat.

Based on the preceding, I argue the elevational shifts I observed are attributable either directly to climate change or to changes in the composition and structure of habitat caused by climate change and/or atmospheric deposition. An alternative hypothesis, however, suggests that range shifts could also be caused by population level processes. Under this hypothesis, population increases cause individuals to move into previously unoccupied locations, albeit of lower quality, and population declines can cause the abandonment of lower quality habitat often found at the edges of a species distribution (Thomas and Lennon 1999). My results do not support this alternative hypothesis. Of the 16 species in this study that showed evidence of range expansion (i.e. boundary shifting away from its center of occurrence), 15 (94%) had populations that were either decreasing or stable, contrary to expectations if range shifts were associated with population trends. Only two of the 19 species that exhibited elevational shifts were consistent with the hypothesis that range shifts could be due to regional population changes. Swainson's thrushes increased according to the BBS and expanded their range downslope, and white-throated sparrows populations decreased and their upper elevational boundary contracted.

Recent developments in modeling species occupancy and abundance have highlighted the importance of accounting for imperfect detection probabilities during data acquisition because perceived differences in abundance among treatments or conditions could be due to differences in detectability (MacKenzie 2006b, Royle and Dorazio 2008), particularly when using monitoring data over a long period of time to test for changes in a species geographic range (Tingley and Beissinger 2009). Correction for imperfect detection probabilities was not possible for my analyses because these models require replicate surveys within a season, and the surveys used for this study were only conducted once per breeding season. It is possible to use spatial replicates, however for this study that would have required summarizing data at the transect level and for this analysis it was essential to associate occurrence at the site level to acquire elevational occurrence. Fortunately, detailed analyses of repeated count data for Montane birds in the White Mountains conducted as part of a separate investigation show that detection probability is not affected by elevation or habitat and that for many of the species exhibiting range shifts detection probabilities were high (Chapter 1). Thus, there is no reason to believe that heterogeneous detection probabilities were responsible for the patterns found in this study.

The consistent elevational shifts across multiple species within the low and high elevation groups demonstrated in my study suggest that these species are responding similarly to some underlying, large scale environmental change. The direct or indirect effects of the changing climate over the course of this study offer plausible explanations for the elevational range shifts I observed. Future studies can work to determine the temporal scale at which climate may alter the distribution of species and then begin to

more closely link those climate data to shifting species' ranges. In addition, studies addressing the underlying mechanism of such elevational range shifts can provide significant insight into the potential environmental changes driving range boundary shifts. For example, determining the extent to which habitat or temperature is limiting montane species ranges would aid in any conclusions regarding causal mechanisms driving range shifts. Research examining demographic components of species with shifting ranges may also reveal responses to environmental change that is not detected with only the examination of distribution (Van Horne 1983, Schlaepfer et al. 2002). With the apparent increase of species using the transition zone as a result of low elevation species increasing their elevational boundary and high elevation species decreasing their elevational boundary, understanding the role of competition in shaping montane bird communities becomes increasingly important.

The findings of this research contribute to the growing body of evidence that anthropogenically induced environmental change is altering the distribution of species. Although prevailing theory states that species will respond to the changing climate by shifting their distributions polewards and increasing in elevation, my research has highlighted the need to apply this understanding with caution. In addition to climate change, other large scale anthropogenic stressors, such as atmospheric deposition (Hames et al. 2002) may be contributing to the changes in the distribution of these species. For at least the immediate future, elevations lower than what may have been previously thought, namely the transition zone between the montane boreal forest and northern hardwoods, could be important for the conservation of some montane birds. I hypothesize that the lower margins of the montane spruce-fir is increasing in suitability

for montane species because of increased dominance of fir associated with declines in spruce. However, ultimately the upward shift in northern hardwoods will encroach on both spruce and fir. Thus, the higher elevations of the montane boreal forest should remain a high priority for the conservation of montane bird species.

Table 2.1: Least squares regression results, testing changes in bird survey elevations over time within each 100 m elevation band between 700 and 1500 m asl from 1993 through 2009.

Elevation Band (m asl)	*t*	Df	*P*
700 – 800	0.166	35	0.869
801 -900	0.206	290	0.837
901 -1000	0.313	963	0.755
1001 – 1100	-0.708	1344	0.480
1101 – 1200	-0.050	1623	0.960
1201 - 1300	-0.614	1314	0.540
1301 – 1400	0.331	597	0.741
1401 - 1500	-0.405	131	0.686

Table 2.2: Change in elevation (m) between 1993 and 2009 for the lower elevation boundary (10th percentile of a species elevation distribution), center of occurrence (mean of a species elevation distribution), and upper elevation boundary (90th percentile of a species elevation distribution) of montane birds. Intercept and slope estimates were taken from linear-mixed models and inserted into the linear equation to derive elevation change. A nonparametric bootstrap procedure (10,000 samples) was implemented to derive 95% CI. Estimates in bold indicates that 95% CI do not include zero. All low elevation species have elevation distribution modes <750 m and are arranged taxonomically. High elevation species are ordered by their elevation distribution modes. Continued onto next page.

Elevation	Species	Percentile of elevation distribution					
		0.1		Mean		0.9	
		Δ Elevation	95% CI	Δ Elevation	95% CI	Δ Elevation	95% CI
Low							
<750m	Black-capped chickadee	-	-	**-44.24**	**-87.77- -3.29**	**-154.13**	**-318.96- -6.50**
<750m	Hermit thrush	-	-	**62.60**	**8.68-131.06**	**253.42**	**117.02-619.43**
<750m	Red-eyed vireo	-	-	11.28	-70.61-131.71	*	*
<750m	Black-throated green warbler	-	-	17.09	-10.44-43.35	95.92	-4.05-148.05
<750m	Black-and-white warbler	-	-	**184.48**	**25.08-317.98**	265.72	-298.76-394.77
<750m	Black-throated blue warbler	-	-	**77.65**	**9.99-145.31**	196.03	-35.57-300.32
<750m	Canada warbler	-	-	149.77	-104.90-309.29	*	*
<750m	Blackburnian warbler	-	-	**170.58**	**18.88-272.97**	**218.75**	**87.28-1025.36**
<750m	American redstart	-	-	**130.59**	**57.87-202.65**	**308.20**	**48.00-449.61**

<750m	Ovenbird	-	-	84.92	-11.54-142.25	148.68	-76.70-462.56
High							
835m	Magnolia warbler	-5.58	-28.16-16.38	7.62	-9.15-24.89	**41.06**	10.45-72.40
979m	Swainson's thrush	**-33.09**	-52.07- -13.47	-6.48	-23.05-10.52	13.89	-9.17-37.10
987m	Winter wren	**-21.33**	-35.81- -7.15	**-14.17**	-28.31- -0.32	-15.99	-30.83-0.12
1046m	Yellow-bellied flycatcher	-11.20	-29.41-8.14	-5.69	-20.19-8.90	-22.05	-44.42-0.66
1079m	Nashville warbler	**-24.53**	-43.36- -7.43	-7.43	-35.24-19.17	50.94	-44.71-127.14
1113m	Blackpoll warbler	-11.30	-21.84-0.02	-1.87	-11.45-7.82	9.11	-0.003-18.55
1232m	Yellow-rumped warbler	**-13.89**	-26.14- -0.96	-1.01	-12.85-10.85	1.75	-10.89-14.05
1240m	Boreal chickadee	2.21	-42.11-51.95	4.46	-17.46-26.14	-10.09	-36.71-28.85
1367m	White-throated sparrow	2.60	-6.86-13.65	3.10	-8.47-14.84	-10.94	-22.21- -0.12
1416m	Bicknell's thrush	-17.40	-44.35-17.01	2.00	-17.12-21.10	13.67	-12.40-32.76
1500m	Dark-eyed junco	**-30.10**	-48.70- -11.33	-12.07	-27.11-3.23	1.36	-12.41-13.89

*Sample size inadequate for analysis

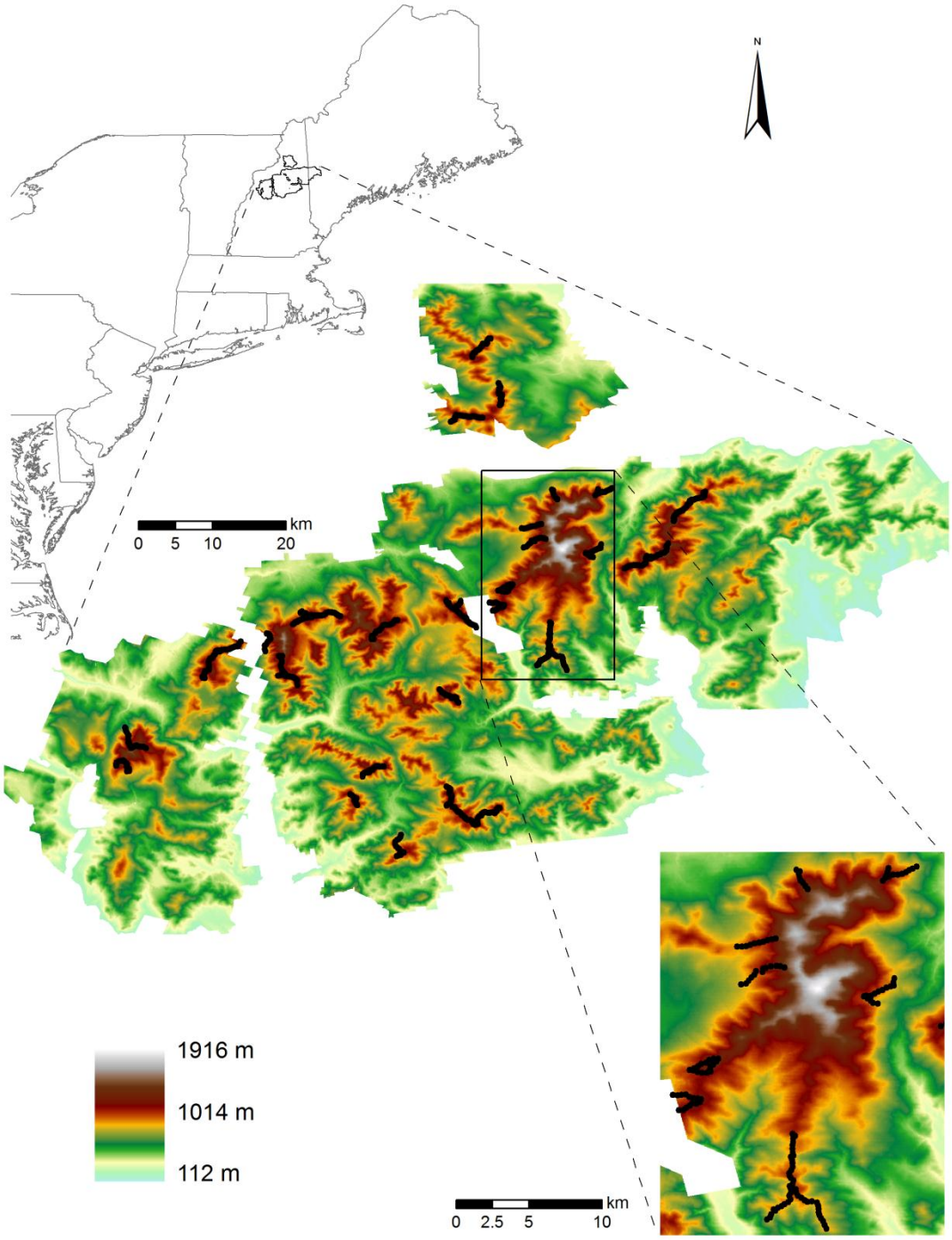

Figure 2.1: Digital elevation model of the study area within the White Mountian National Forest, NH, USA. Black lines in the first inset identifiy transect locations. Black dots in the second inset are bird survey locations.

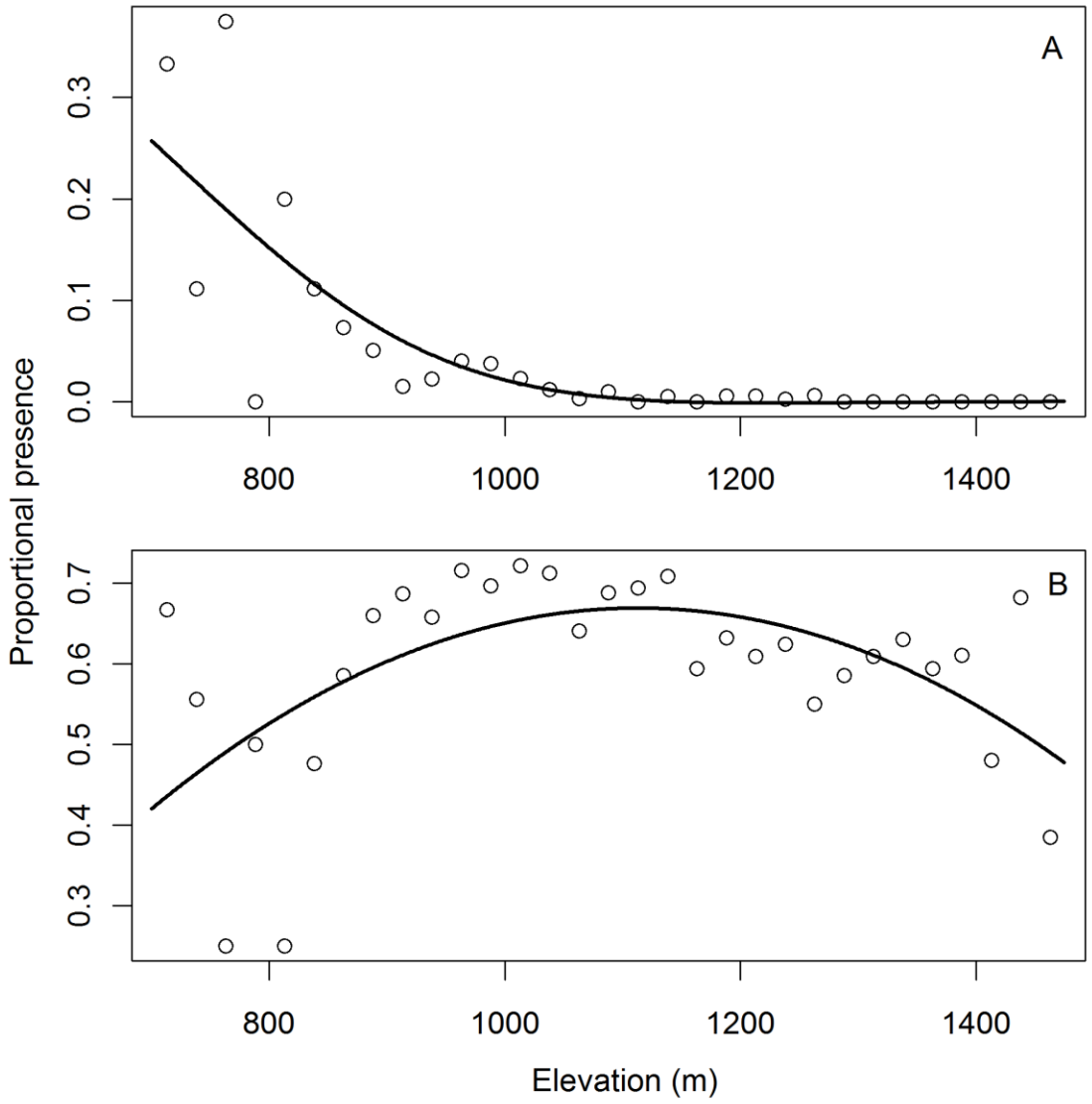

Figure 2.2: Examples of elevation distributions for (A) a low elevation species (black-throated blue warbler) and (B) a high elevation species (blackpoll warbler). Fitted lines are from regression models.

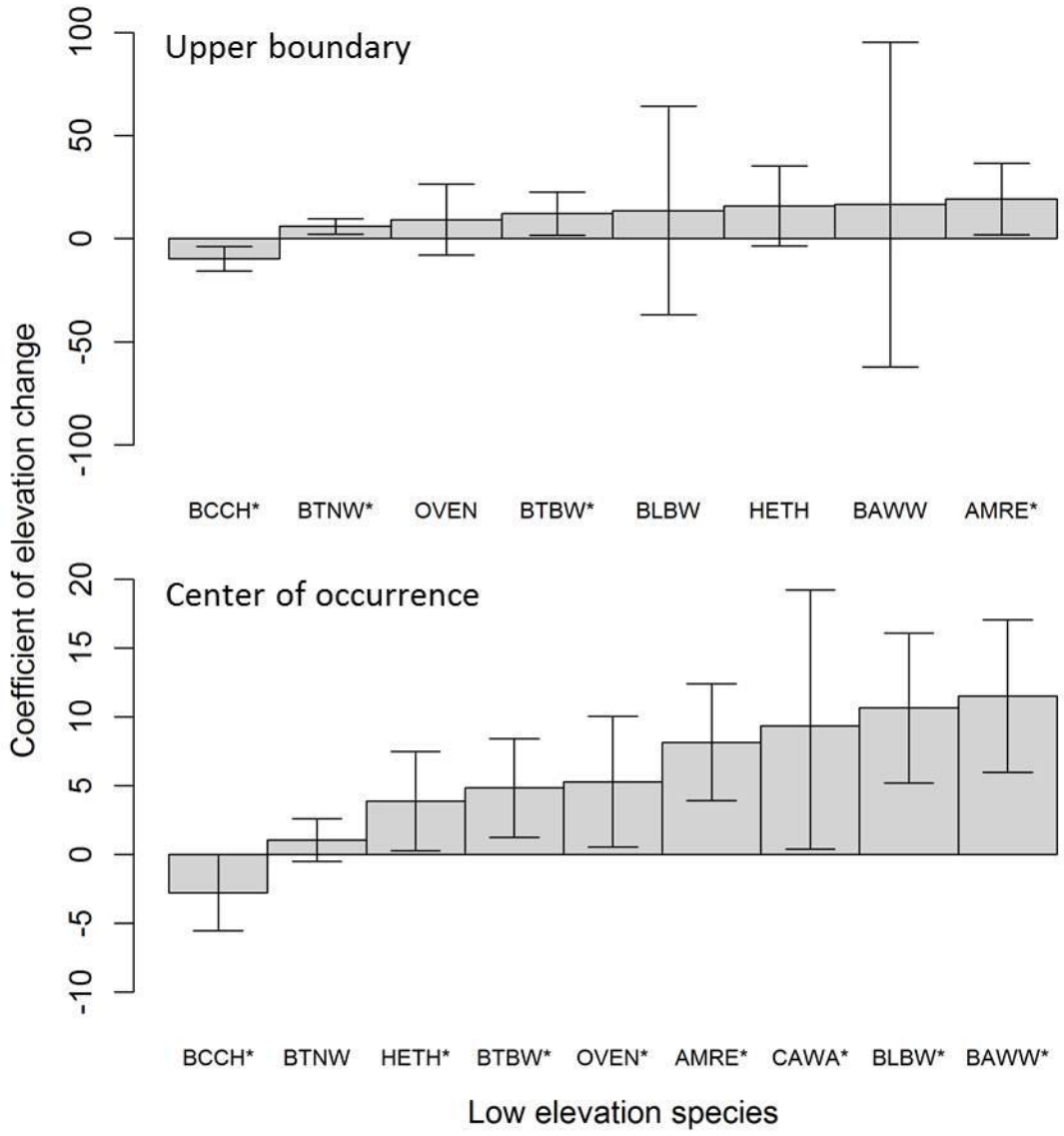

Figure 2.3: Coefficient estimates and 95% CI from linear-mixed models for the change in elevation between 1993 and 2009 for low elevation species. Positive coefficients indicate an elevation increase while negative coefficinets indicate an elevation decrease. Asterisks indicate that the 95% CI do not include zero and that the fixed coefficient estiamte for change in elevation over time is different than zero ($P < 0.05$). AMRE=American redstart; BAWW=balck-and-white warbler; BCCH=black-capped chickadee; BLBW=blackburnian warbler; BTBW=black-throated blue warbler; BTNW=black-throated green warbler; CAWA=Canada warbler; HETH=hermit thrush; OVEN=ovenbird.

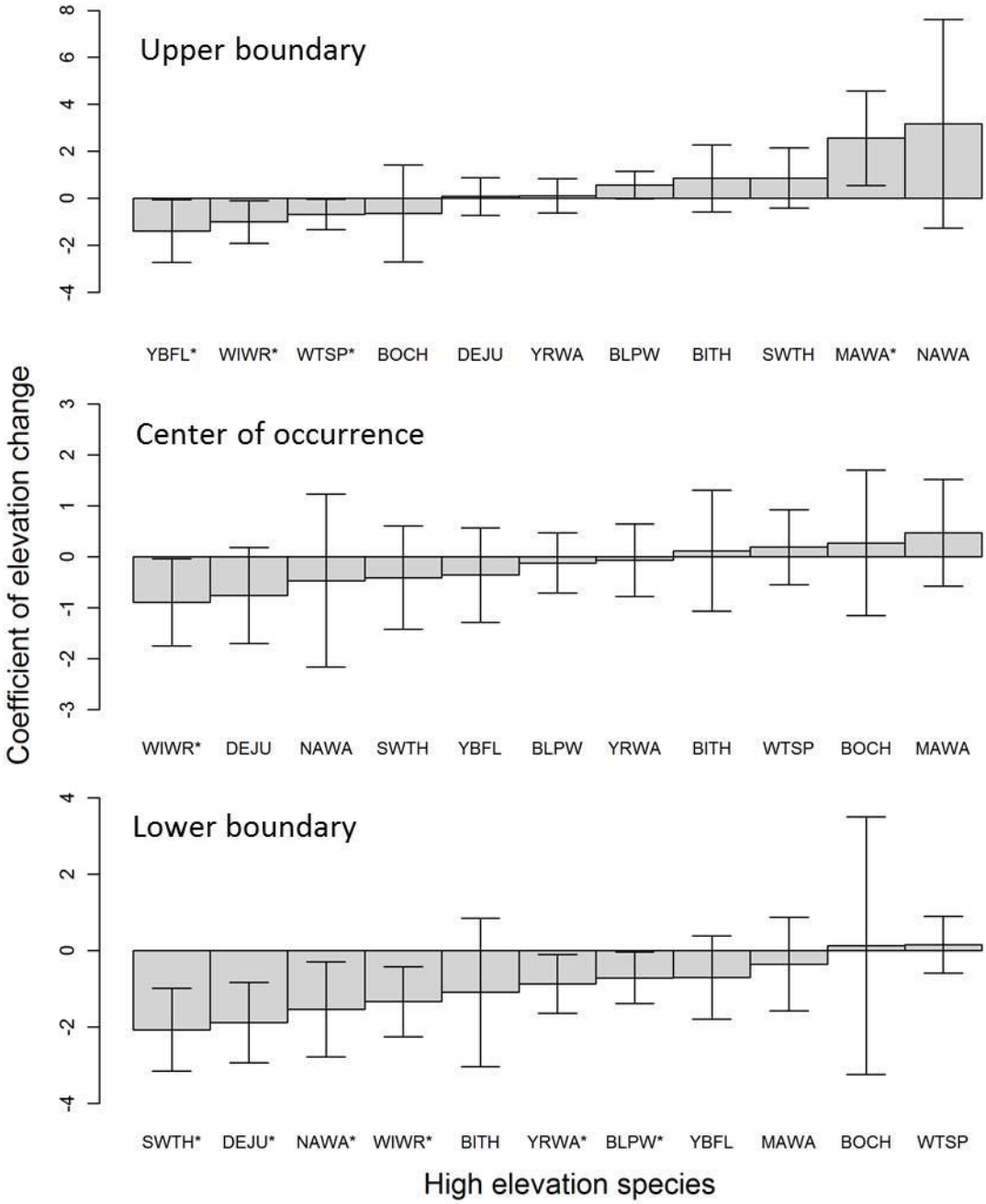

Figure 2.4: Coefficient estimates and 95% CI from linear-mixed models for the change in elevation between 1993 and 2009 for high elevation species. Positive coefficients indicate an elevation increase while negative coefficinets indicate an elevation decrease. Asterisks indicate that the 95% CI do not include zero and that the fixed coefficient estiamte for change in elevation over time is different than zero ($P < 0.05$). BITH=Bicknell's thrush; BLPW=blackpoll warbler; BOCH=boreal chickadee; DEJU=dark-eyed junco; MAWA=magnolia warbler; NAWA=Nashville warbler; SWTH=Swainson's thrush; WTSP=white-throated sparrow; WIWR=winter wren; YBFL=yellow-bellied flycatcher; YRWA=yellow-rumped warbler.

CHAPTER 3

BLACKPOLL WARBLER (*Setophaga striata)* BREEDING ECOLOGY ALONG AN ELEVATION GRADIENT: CONSEQUENCES OF TEMPORAL AND SPATIAL VARIATION IN CLIMATE

3.1 Introduction

Climate is important for determining a species' distributional limits as well as the quality of habitat within those limits. Species distributions are restricted by their climatic niche envelop; that is, a range of climatic conditions they are distributed across (Wiens et al. 2009). Climate can directly constrain a species' distribution and influence habitat quality through physiological constraints (Newton 1998). For example, although suitable resources may be present at a location, a species may be unable to benefit from them because they are unable to adequately thermoregulate given the climatic conditions at the location. Climate can also indirectly determine habitat quality by defining the composition and structure of the plant community upon which the species is dependent (Able and Noon 1976, Martin 2007). It is difficult to untangle the complicated role of climate, habitat, and competition when defining a gradient of habitat quality within a species' distribution and this question has inspired several classic ecological studies (e.g., Grinnell 1914, 1917, MacArthur 1957, Hutchinson 1959, Terborgh 1971). The dramatic recent changes in global climate have now further complicated these intertwined relationships and its effect on these processes is still relatively unknown.

The temporal and spatial variations of climate are both important perspectives for understanding how wildlife will respond to future climatic conditions. Because substantial climatic change has occurred over a relatively short time period, one effective strategy for examining the implications of climate change has been to observe the response of wildlife to historic temporal variation in climate (Root et al. 2003). Some temporal responses to climate change that have been documented include changes in the onset of breeding (Torti and Dunn 2005) and migration (Studds and Marra 2011), species distributions (Zuckerberg et al. 2009), body size (Van Buskirk et al. 2010), synchrony with food resources (Both et al. 2005) and reproductive success (Crick 2004). However, the spatially compressed climatic conditions that often exist within an ecosystem along an elevation gradient also offer an opportunity to examine species' response to climate variations.

The dramatic changes in climate with increasing elevation (i.e., cooler, wetter, and windier) cause marked changes in the structure and composition of forests within a relatively small spatial extent (Reiners and Lang 1979, Cogbill and White 1991). This spatial variation in climate and the associated changes in habitat often correspond to a gradient in habitat quality for some species (Rodenhouse et al. 2003, Betts et al. 2008). For these species, lower elevations typically correspond to low quality habitat and are associated with warmer drier climates. In general, the warmer drier climates at lower elevations represent the future conditions predicted to occupy a greater extent of the elevation gradient with climate change (Rodenhouse et al. 2008). Therefore, high elevation ecosystems and the species that occupy them are particularly vulnerable to climate change because the climatic conditions and habitats associated with lower

elevations are predicted to shift upslope (Sekercioglu et al. 2007). In montane spruce-fir forests of northeastern North America the climate of the lower elevation ecotone has warmed significantly (Seidel et al. 2009) and the lower elevation boundary of this ecosystem has shifted upslope approximately 100 m over the last 40 years (Beckage et al. 2008). It is becoming clear that montane ecosystems will occupy progressively less area over time (Lambert et al. 2005, Rodenhouse et al. 2008), however, it remains unclear whether or not a gradient in habitat quality exists within this ecosystem and if it coincides with that spatial climatic variation associated with elevation.

Habitat quality can be defined as the contribution to population growth from a given set of habitat characteristics (Fretwell and Lucas 1970, Wiens 1992). Habitat-specific, demographic measures such as density and reproduction can be reliable measures of habitat quality (Johnson 2007). Although density or occupancy can sometimes be a misleading indicator of habitat quality (Van Horne 1983), under some circumstances such as under the ideal free distribution of Fretwell and Lucas (1970), higher quality habitats may also have higher densities. In addition, higher quality habitats tend to have higher nest success, fledge more young per capita and have lower nest predator abundance (Holmes 2011). Males occupying higher quality habitat tend to be more successful at attracting a mate and tend to be older (Cody 1987, Newton 1998, Holmes 2011). Therefore, across habitat conditions, along a gradient of habitat quality, individuals contribute varying amounts to general population dynamics. For vulnerable ecosystems such as montane forests, with potentially steep gradients in habitat quality, it is important to understand whether or not all conditions, driven by spatial variation in climate along the elevation gradient, are contributing to population stability or growth.

High elevation spruce-fir forests of northeastern North America are believed to be vulnerable to several anthropogenic stressors and several species identified as indicators of montane spruce-fir habitat have recently exhibited significant population declines (King et al. 2008, Lambert et al. 2008). Climate change in particular, has been identified as a significant threat to montane ecosystems and has been linked to the extinction (Pounds et al. 1999) and displacement (Konvicka et al. 2003, Wilson et al. 2005, Pauli et al. 2007, Raxworthy et al. 2008) of many montane species due to the upslope shift of warmer conditions. As a consequence, species dependent on montane ecosystems are considered to be "early warning" sentinels of how species may react to the changing climate. Although much of the research has focused on changes in montane species' distribution, still little is known about how species may be performing within their elevational range and whether that performance varies temporally or spatially with climate.

The objectives of this study were to examine how temporal and spatial variation in climate affects the reproductive ecology of a montane forest, neotropical migratory songbird, blackpoll warbler (*Setophaga striata*). Specifically, I tested whether variations in precipitation and temperature from 1994 to 2003 influenced the onset of blackpoll warbler (hereafter blackpoll) breeding and daily nest survival at two sites in the Green Mountains of Vermont. I then tested whether the spatial climatic variation along an elevation gradient on Mount Jefferson, New Hampshire influenced blackpoll habitat quality. I measured blackpoll abundance, age, mate pairing capacity, daily nest survival, fecundity and the occupancy of an abundant nest predator and tested whether these measures of habitat quality varied with spatial variation of climate associated with the

elevation gradient. I hypothesized that temporal variation in climate would influence blackpoll nest initiation dates and potentially daily nest survival. I also hypothesized that the strong variation in climate along the elevation gradient which drives significant changes of forest structure and composition (Reiners and Lang 1979) would result in a gradient of habitat quality for blackpolls, such that measures of blackpoll abundance and reproductive success would increase with elevation.

3.2 Methods

3.2.1 Study area

Data for this study were collected at two locations in the Green Mountains, Vermont; Stratton Mountain (43°05'N, 72°55'W) and Mount Mansfield (44°32N, 72°49'W), and along one mountain range in the White Mountains, NH; The Presidential Range (N44°7' to N44°21' W71°27' to W71°14'; Figure 3.1). Blackpoll data from the Green Mountains were collected from 1994 through 2003 and were used to test the effect of temporal climate variation on blackpoll nest initiation and daily nest survival. Data from the Presidential Range were collected from 2006 through 2009 and were used to examine whether a gradient of blackpoll habitat quality exists along an elevation gradient that corresponds to spatial variation in climate. Data collection ranged in elevation from approximately 880 - 1,200 m asl. Because all three sites are of similar latitude, the elevation of the spruce-fir/deciduous forest ecotone and the rate of decrease in canopy height with elevation is generally similar for at all three locations (Cogbill and White 1991).

In the Green and White Mountains, forests exhibit distinct compositional and structural changes with increasing elevation (Reiners and Lang 1979, Cogbill and White 1991, Beckage et al. 2008). For both the Greens and Whites, below approximately 750 m asl northern hardwood communities dominate. This community is characterized by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula lutea*). Above 750 m asl, red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*), softwood species associated with the boreal forest, increasingly mix with hardwoods until approximately 1,000 m asl, where the boreal forest begins to dominate. Above 1,000 m asl, mountain paper birch (*Betula cordifolia*), mountain ash (*Sorbus americana*), mountain maple (*Acer spicatum*), and pin cherry (*Prunus penslvanica*) are the only hardwoods interspersed within the spruce-fir matrix (Lee et al. 2005). As softwoods become dominant with increasing elevation, canopy height begins to decrease. For three areas in the White Mountains (including the Presidential Range), Reiners and Lang (1979) found that canopy height was approximately 13.3 m near 1,200 m asl and decreased to 3.2 m just below the krummholz zone. The krummholz zone is just below treeline (approximately 1,500 m a.as.l.) and is a short, thick, tangle of predominantly balsam fir. These abrupt and distinct changes in the composition and structure of the montane forest are attributed to significant changes in climate with increasing elevation (Reiners and Lang 1979).

Temperature and precipitation have significant spatial variation with increasing elevation in northeastern North America (Reiners and Lang 1979, Sabo 1980, Barry 1992). Temperature decreases substantially with increasing elevation. The mean annual temperature (1992-2009) at Pinkham Notch, NH (612 m asl) was 4.6°C while the mean

annual temperature (same years) on the summit of Mount Washington, NH (1,914 m asl) was -2.4°C and the distance between the two locations is < 5 km (NOAA Satellite and Information Service 2011). Orographic cooling causes a strong increase in precipitation with increasing elevation. The average annual precipitation (1992-2009) on the summit of Mount Washington was 2,324 mm and average annual precipitation for Pinkham Notch was 1,560 mm (NOAA Satellite and Information Service 2011). Wind, rime ice and condensation are also important climatic factors that increase in elevation (Reiners and Lang 1979). Together, these climatic factors create a set of fine and course-scaled disturbance processes that shape the structure and composition of montane spruce-fir forests (Sprugel 1976, 1984, 1991, Reiners and Lang 1979, Sprugel and Bormann 1981).

3.2.2 Blackpoll warbler (*Setophaga striata*)

The blackpoll warbler (Figure 3.2) is a neotropical migratory passerine that breeds in boreal forests from Alaska to northeastern North America. At the southern part of its range, including the White and Green Mountains, it is limited to montane and coastal spruce-fir forests. Where habitat is suitable, blackpolls can reach densities of up to four pairs per hectare and territories in the U.S. portion of their distribution typically range between 0.4 and 0.8 ha (Hunt and Eliason 1999). Blackpolls are typically socially monogamous and in the study area fledge only one brood a year. Blackpolls are most known for their extraordinary migration route where they move east across North America and depart from the coast, traveling nonstop for up to 88 hours to South America (2,500 km to 3,500 km) over the Atlantic Ocean. Although blackpolls may be one of the most abundant warblers of North America, they also exhibited one of the most

rapid population declines of any songbird from 1980 to 2007 of 9.7% per year (Sauer et al. 2008). The cause of such precipitous declines is still undetermined, but habitat loss throughout the annual cycle, atmospheric deposition, tower kills, and climate change are all potential contributors.

3.2.3 Blackpoll warbler nest initiation, nest survival and temporal variation in climate

Blackpoll nest initiation data were collected on Mount Mansfield and Stratton Mountain of the Green Mountains, Vermont (Figure 3.1). Data were collected from 1994 to 2008. Blackpoll nests were located by systematic searches of suitable vegetation as well as by following individuals displaying nesting behavior (e.g., carrying nest material or food). When possible, nests were monitored every third day and nest success was determined following the recommendations of Manolis et al. (2000). Nest initiation was considered the date for which the first egg was laid. When nests were found after the nest initiation date, initiation dates were back-calculated. Initiation dates were recorded as days past May 20. For each year at each site, data were summarized as the mean date of first nest attempt for all nest initiation dates.

Climate data was obtained from the Mount Mansfield Summit Meteorology Station via the Vermont Monitoring Cooperative from 1994 to 2008 (Wright 2010). Weather data is recorded daily at the station which is at an elevation of 1,189 m asl Specifically, I acquired daily maximum temperature and total daily snow for the month of May, when blackpolls typically arrive to begin breeding at my study sites. Weather immediately preceding or during arrival on the breeding grounds has been shown to be

important determinants for breeding passerines (Dolenec 2007, Potti 2009, Mazerolle et al. 2011). May precipitation was also considered; however, it was confounded with snowfall and inspection of scatter plots and evidence in the literature (Decker and Conway 2009) implied that snowfall could be an important predictor of montane bird nest initiation. Data were summarized as the average daily maximum temperature, and the average daily snow total. These data were then used in relation to blackpoll nest initiation and daily nest survival to determine the extent to which temporal variation in climate affects blackpoll breeding.

3.2.4 Blackpoll warbler demography and spatial variation in climate

3.2.4.1 Blackpoll warbler abundance

Surveys were conducted along ten trails throughout the Presidential Range and Crawford Notch region of the White Mountain National Forest (N44°7' to N44°21' W71°27' to W71°14'), encompassing approximately 46,000 ha. Trails had sufficient length within the montane spruce-fir forest, typically between elevations of 750 m asl and treeline (~1500 m asl), so that four survey locations could be established on each trail with distances between survey locations no less than 250 m and no more than 1 km. For each survey on the trail, two other survey locations were established; one at 200 m and one at 400 m perpendicular to the trail. At some locations, either topography or trail density precluded the establishment of surveys 400m from the trail. Surveys were conducted in 2006 and 2007. In 2007, 113 sites were surveyed; 40 surveys were located on trails, 40 were located 200 m from a trail, and 33 were located 400 m from a trail. In

2006, the same locations were surveyed, however only 10 of the locations were surveyed at the 400 m distance.

Point count surveys in both years were conducted three times at each location between 6 June and 17 July by one of four trained observers. Each survey consisted of a 10-minute point count during which all birds and red squirrels (*Tamiasciurus hudsonicus*) seen or heard were recorded as being either within 50 m of the survey location or >50 m of the survey location. Only singing males and red squirrels within 50 m were used for analysis. Surveys began at dawn and continued until 1100 hours, weather permitting. The first round of surveys within each year started at lower elevation sites and proceeded upslope, the second survey began at the highest elevations and proceeded downslope, and the last survey of the year followed the order of the first. Weather was given a score of one through four for each survey, where a score of one indicated clear conditions and a score of four indicated clouds with some drizzle. Surveys were not conducted if weather conditions warranted a score higher than four. Wind was also given a score of one through four, where a one indicated calm conditions and a score of four indicated that wind was strong enough to move tree branches, but not the main trunk of the tree. Surveys were not conducted if wind conditions warranted a score higher than four.

3.2.4.2 Blackpoll warbler reproductive ecology

The remaining blackpoll demographic variables were collected on Mount Jefferson (44°17'N 71°20'W) of the White Mountains, New Hampshire (Figure 3.1) on a ~30 ha site ranging in elevation from 900 m to 1,100 m asl from 2006 to 2009. Attempts were made to capture all breeding males on the plot, which was gridded at 25 m intervals.

Upon capture, birds were individually marked and an estimate of age was recorded. Age was classified as either after second year (ASY), second year (SY), or after hatch year (AHY). Territories of each male on the plot were then mapped relative to the grid with GPS units. Territories were continuously mapped throughout the breeding season such that each territory was visited for ≥30 minutes every third day. Every territory was visited no less than 12 times over the course of a season. Territory boundaries were entered into a GIS (ArcGIS 10; ESRI 2011) and the elevation of each territory's centroid was recorded. At the end of the breeding season each territory was given a reproductive index score to quantify the varying stages of the reproductive cycle a male achieved (Vickery et al. 1992). The reproductive index I used was a modification of the index developed by Vickery et al. (1992). The scoring followed that of Vickery's index for single-brooded species, with the only modifications from Vickery's index was a score of 6 was given to polygamous males (Table 3.1).

Blackpoll nests were located by the same methods described above for the Green Mountain sites. Once nests were located, I monitored them every third day and recorded nest contents. Care was taken to approach the nest from different directions and if predators (e.g., gray jay [*Perisoreus canadensis*]) were in the area the nest was checked later in the day. Upon nest completion, I searched for fledglings near the nest or being fed by a known parent to confirm nest success because most of the potential nest predators often do not disturb the nest (King and DeGraaf 2006). Seasonal fecundity was measured as the number of young fledged per female (Holmes 2011).

To examine the effect of spatial variation of climate and the climate-driven structural and compositional habitat variation on blackpoll demography, I used elevation

as a proxy of this variation. Elevation is a valid proxy for spatial climate variation for reasons discussed in Section 3.2.1. After territories were submitted to a GIS, a 30 m cell, digital elevation model was used to determine the elevation of the centroid of each territory (ESRI 2011). Elevation of each nest found was recorded in the field with a GPS and confirmed later with the digital elevation model in GIS.

3.2.5 Data analysis

3.2.5.1 Blackpoll warbler nest initiation, nest survival and temporal variation in climate

I used an ANOVA model to test whether initiation dates varied between the Mount Mansfield and Stratton Mountain sites. Upon confirming that initiation dates were not significantly different between the two sites ($F_{1,141} = 0.01$, $P = 0.94$), I used ordinary least squares regression and considered models with predictor variables including May daily snow only, May daily maximum temperature only and both. Mean blackpoll first nest initiation dates were the dependent variable in each model. I used AIC_c to compare models and considered those with $\Delta AIC_c < 2.0$ for interpretation. I then used the logistic-exposure model described by Shaffer (2004) to test whether these climate variables had a significant influence on estimates of daily nest survival. The logistic-exposure model is a generalized linear model with a binomial error distribution and a modified link function: $g(\theta) = \ln [\theta^{1/t}(1 - \theta^{1/t})]$, where θ is the nest survival estimate and t is the observation interval in days. To calculate exposure days and nest fate I followed recommendations of Manolis et al. (2000). To calculate exposure days for unsuccessful nests I used the midpoint between the final two nest checks. I used AIC_c to

compare models with the climate variables to the null model and only considered climate models if they had stronger support than the null model (Burnham and Anderson 2002). I also performed a likelihood ratio test between the null model and climate models to confirm differences between them. Regression models were fit using the *glm* function in the R 2.14.0 package glm.

3.2.5.2 Blackpoll warbler demography and spatial variation in climate

I used the *N*-mixture model (Royle 2004) to examine the response of blackpoll abundance to elevation while accounting for the effect of imperfect detection probabilities. The *N*-mixture model estimates two parameters λ and p, where λ is the mean of the Poisson distribution used to represent the distribution of the actual number of birds at a survey location (N_i) and therefore, estimates abundance. The probability of detecting N_i during a sampling event is p. It is likely that individuals move into and out of survey locations between sampling events within a season, therefore λ is defined as the mean number of territorial males that used each site over the course of the season (Chandler et al. 2009a). Elevation, a quadratic term for elevation and year were included as site-level predictors in all candidate models. Year was included because data were collected over two years and I wanted to assess each year independently. Time of day, weather, wind, date, and observer were considered as detection probability covariates. I used AIC_c to compare and select models with small sample sizes to choose the best combination of detection probability covariates (Burnham and Anderson 2002). I considered all combinations of covariates that performed better than a model without covariates of p. I considered models with $\Delta AIC_c < 2.0$ to be strongly supported and used

Nagelkerke's R^2 to approximate the variation explained by each model (Nagelkerke 1991, Chandler et al. 2009a). Terms in the model were considered significant if the 95% confidence interval of their coefficient did not include zero. I used the *pcount* function in the unmarked package in R-2.14.0 to run the *N*-mixture models.

For demographic data recorded on Mount Jefferson, I first used an ANOVA to determine that territory elevation of SY and ASY males did not differ between years ($F_{1, 47} = 2.39$, $P = 0.23$) and then compared the mean elevation and 95% confidence intervals (CI) of territory centroids for SY and ASY males across years. I considered mean elevation of territories of SY and ASY birds to be significantly different at $\alpha = 0.05$ if 95% CI's did not overlap. Because territory elevations did not vary by year I also pooled reproductive index scores across years and used a generalized additive model (GAM) to test whether there was a relationship between blackpoll pairing success and elevation. I used the package *mgcv* in R-2.14.0 to fit the GAM to the data using the Gaussian error family. GAMs are fit using an interative least-squares method with non-parametric smoothing functions and the model is penalized with each smoothing parameter which are estimated by minimizing the generalized cross validation criterion (Wood 2006, Crawley 2007).

I used the previously described logistic-exposure model to analyze the relationship between daily nest survival and elevation. I used AIC_c to compare the model with elevation as a predictor to the null model and considered the elevation model supported if its AIC_c was < that of the null model (Burnham and Anderson 2002). I also performed a likelihood ratio test between the null model and the elevation model to

confirm differences between them. I then used least squares regression to test if blackpoll fecundity increased with increasing elevation.

Because the majority of blackpoll nest failures were due to predation and red squirrels are believed to be one of the primary montane songbird nest predators I used a single season occupancy model (MacKenzie et al. 2002, 2006) to estimate red squirrel occupancy across the elevation gradient in 2007. This model estimates two parameters Ψ and p, where Ψ is the probability that a site is occupied and p is the probability of detecting an individual during a sampling event. It is likely that the survey area is not closed to movement of individuals between surveys, therefore Ψ is interpreted as the probability of an individual occupying the sampling area at some point during the breeding season. Elevation was included in the model as the only site-level covariate and I considered time of day, weather, wind, date, and observer as potential detection probability covariates. I used the same criteria to assess candidate models as described for *N*-mixture models. I used the *occu* function in the unmarked package in R-2.14.0 to run the single season occupancy models.

3.3 Results

3.3.1 Blackpoll warbler nest initiation, nest survival and temporal variation in climate

From 1994 through 2003 at the Mount Mansfield Summit Meteorology Station the range of mean daily precipitation for the month of May was 3.56 mm to 10.16 mm, with a mean of 6.10 mm. The range of mean daily snowfall was 0 mm to 23.00 mm with

a mean of 6.35 mm and the range of mean daily maximum temperatures was 6.33° C to 16.56° C with a mean of 10.83° C.

One hundred and fifty-four blackpoll nests were located and used for analysis between 1994 and 2003, 91 nests on Mount Mansfield and 63 nests on Stratton Mountain. Models containing daily maximum temperature to predict blackpoll nest initiation were not supported ($\Delta AIC_c > 2.0$). The linear model containing only daily snowfall in May was the model with most support. Blackpolls initiated nesting later in years with greater May daily snowfall ($R^2 = 0.60$, $P = 0.01$; Figure 3.3). For years with below average snowfall in May, the earliest initiation dates occurred in years with above average maximum daily temperatures and later initiation dates occurred in years with below average temperatures (Figure 3.3). The null logistic-exposure model was supported over models with climate variables and this lack of support was confirmed with the likelihood ratio tests ($P > 0.10$), suggesting that May snow and temperature are not important for determining blackpoll daily nest survival.

3.3.2 Blackpoll warbler demography and spatial variation in climate

Blackpolls were detected 677 times over the two years that point count surveys were conducted. There was some model uncertainty for detection probability (p) covariates among models with strong support (Table 3.2). I found that detection probability was higher with low wind, good weather, earlier in the breeding season and earlier in the day (Table 3.2). For all supported models, the linear and quadratic terms for elevation were significant (Table 3.2). Blackpoll abundance increased with elevation

reaching an optimum at approximately 1,250 m asl and then declined slightly towards treeline (Table 3.2 and Figure 3.4).

Forty-nine male blackpolls were captured (ASY = 34, SY = 15) on Mount Jefferson between 2006 and 2008. ASY males occupied territories that ranged from 932 to 1,164 m asl and were at significantly higher elevations than SY males which had territories that ranged from 922 to 1,124 m asl (Figure 3.5). Reproductive index scores ranged from 1 to 6 for the 42 blackpoll territories that were monitored. The GAM revealed a significant relationship between elevation and the reproductive index ($P < 0.001$) with 77.6% of the deviance explained. The model fit to the data shows that reproductive index scores rise relatively steeply up to about 1,000 m asl and then level off (Figure 3.6).

Forty-six blackpoll nests were monitored on Mount Jefferson, of which 14 failed. The logistic-exposure model with elevation had strong support over the null model ($\Delta AIC_c = 4.55$) and the likelihood ratio test between these models supported this ($P = 0.01$), indicating that blackpoll nest success increases steeply with elevation and begins to level off at higher elevations (Figure 3.7). The 32 successful nests averaged 3.30 fledglings, ranging from 1 to 5 fledglings per successful nest. Blackpoll fecundity also increased with elevation ($R^2 = 0.18$, $P = 0.007$; Figure 3.8).

Twelve of the 14 failed nests were due to predation. Red squirrels were detected at 67 of the 113 sites that were surveyed. Models including elevation for predicting red squirrel occupancy were strongly supported (Table 3.3) and the model with the strongest support revealed that red squirrel occupancy declines with increasing elevation (Figure 3.9). Temperature and wind were most important for detecting red squirrels (Table 3.3).

3.4 Discussion

Species inhabiting montane ecosystems have been identified as being particularly vulnerable to the effects of climate change (Rodenhouse et al. 2008). To date, the vast majority of studies have focused on upslope encroachment of lower elevation species and to some extent, elevational range contraction of high elevation species. This study is the first to examine the underlying mechanisms of how climatic variation influences the reproductive success and demography of a Neotropical-Nearctic migratory songbird. By examining the role of temporal climate variation, this study sheds light on potentially immediate reactions of blackpolls to annual variation in climate. The gradient in habitat quality associated with elevation-driven, spatial variation in climate explains the relatively poor reproductive performance found at lower elevations and highlights potential mechanisms for range contraction of high elevation birds.

In an effort to time breeding with optimal conditions, migratory birds often use environmental cues such as temperature to signal the onset of breeding (Crick et al. 1997, Dunn and Winkler 1999, Mazerolle et al. 2011). The results of this study are the first support the hypothesis that montane birds in northeastern North America respond to environmental cues that are susceptible climate driven changes, to initiate breeding. Blackpolls initiate nesting later in years when there is more snowfall in May and typically initiate nesting earlier in years with less snowfall (Figure 3.4). There is also evidence to suggest that for years with Mays that have below average snowfall, blackpolls are more

likely to initiate nesting earlier in warmer years than in cooler years (Figure 3.4). Long-term climatic trends in the region at similar elevations to this study indicate that Spring (Seidel et al. 2009) and annual (Wright 2009) temperatures are rising. Although measures and predictions of precipitation are less clear (McCain and Colwell 2011), trends from Mount Mansfield suggest that total precipitation and snowfall is also increasing (Wright 2009). These trends have potentially conflicting consequences for future blackpoll nest initiation dates.

My results suggest a potential hierarchy of how blackpoll nest initiation responds to climate. Because May temperature was not supported over May snowfall, it suggests that snowfall is a primary driver in determining blackpoll nest initiation dates. However, in the absence of significant May snowfall, temperature appears to be a secondary determinant of initiation dates. Because migratory birds use climatic cues along the migration route to time arrival on the breeding grounds (Halkka et al. 2011), it is possible that mismatches could occur between cues determining breeding ground arrival and the initiation of nesting. For example, if temperatures along the migration route result in early arrival on the breeding grounds and site-specific May snow is above average, then early-arriving individuals could experience a significant lag between arrival and breeding. It is unclear what the consequences of such a lag may be on breeding success.

Although I did not find a link between nest survival and climate, other studies have found that shifting nest initiation dates due to climate can have important consequences for birds. The plasticity with which birds alter the initiation of breeding typically takes advantage of available resources and can result in increased reproductive output (Crick 2004, Dunn 2004, Halupka et al. 2008), however, shifts in nest initiation

can also have deleterious effects. Early nest initiation, while sometimes beneficial for synchrony with food resources, can mistime a breeders typical avoidance of peak exposure to nest predators causing increased rates of nest failure (Preston and Rotenberry 2006). Furthermore, changes in the timing of nest initiation may expose potential breeders to severe weather events more common in early spring, particularly in high elevation habitats. For example, despite increasing spring temperatures over a 58-year period at a montane site in southwestern Arizona, a late-spring snowstorm resulted in the nest abandonment for 68% of red-face warblers (*Cardellina rubrifrons*) at the site (Decker and Conway 2009). With future climate predictions forecasting increases in the severity and variability in precipitation events (McCain and Colwell 2011), occurrences such as these may pose a significant threat to early-nesting montane birds. Although early blackpoll nest initiation can lead to higher reproductive success (Eliason 1986) and warming trends in the region suggest a potential for earlier initiation dates, catastrophic nest failures, such as those found by Decker and Conway (2009), caused by spring snowfall may negate the potentially positive effects of warmer temperatures.

An understanding of how montane birds perform under varying climate conditions is imperative to defining the potential mechanisms that may cause range shifts or population declines due to climate change. I found evidence for a gradient in habitat quality for blackpolls that is associated with spatial variation in climate along an elevation gradient. This gradient in habitat quality suggests that at the lower elevational boundary, blackpolls are less abundant, have decreased measures of reproductive capabilities, and are exposed to higher occupancy rates of a primary nest predator. All of

which could be potential mechanisms causing future range retraction or population declines.

Climate can directly or indirectly influence the suitability at a given location for birds. It does not appear as though climate (i.e. temperature) is directly limiting blackpoll suitability because despite recent warming (Beckage et al. 2008, Seidel et al. 2009, Wright 2009), blackpolls are expanding their range downslope (Chapter 2). If blackpolls were limited at their lower elevational boundary by warmer temperatures, I would not have found evidence of a downslope shift in their lower elevational boundary (Chapter 2). It is unlikely that blackpolls' thermoregulation is compromised at lower elevations such that reproductive success and demography is altered. Therefore, the gradient in habitat quality is likely driven indirectly by climate through differences in habitat structure and composition, nest predator populations, or increased competition with lower elevation species shifting their range upslope (Chapter 2).

The cooler, wetter, and windier climates with increasing elevation cause a significant change in the structure and composition of montane forests (Cogbill and White 1991). Within montane spruce-fir forests, lower elevations have higher canopies, lower stem densities, fewer natural disturbances and therefore less regeneration, and higher hardwood basal area compared to higher elevations (Reiners and Lang 1979, Sabo 1980, Sprugel and Bormann 1981, Cogbill and White 1991). Able and Noon (1976) found that many montane bird distributions are driven primarily by habitat. Blackpolls as well as other montane spruce-fir specialists, such as Bicknell's thrush (*Catharus bicknelli*), prefer habitats with higher densities of conifers, particularly balsam fir (Eliason 1986, Hunt and Eliason 1999, Rimmer et al. 2001). Therefore, the increased

component of hardwoods and lower densities of conifers at lower elevations provide lower quality habitat for blackpolls.

There are several potential consequences of low quality habitat on blackpoll demography, some of which were supported by my results. Many passerines use habitat cues to assess quality and make decisions about where to attempt breeding (Cody 1987). They are also more likely to have higher sight fidelity where they were reproductively successful the previous breeding season (Newton 1998) and this is the case for female and possibly male blackpolls (Eliason 1986). It is likely that older more dominant males are responding to indicators of habitat quality (i.e., high basal area of conifers) and are establishing territories in areas with higher habitat quality associated with higher elevations. Furthermore, once a male is successful at higher elevations, he may be more likely to return to the same territory the following year. Future research should examine survival rates as a function of the variation of climate across the elevation gradient. My data suggest that younger, less experienced and less dominant males are relegated to lower quality habitat. These are possible explanations for my findings that with increasing elevation, males are older and are more likely to be paired with a female. My findings coincide with the habitat heterogeneity or site dependence hypothesis to describe density-dependent patterns of population regulation (Ferrer and Donazar 1996, Rodenhouse et al. 1997, Ferrer et al. 2008). Under this hypothesis average reproductive success of the population is reduced by the use of less suitable habitat where nest survival and fecundity are reduced.

Forest composition and structure as well as climatic conditions at the lower elevational boundary of blackpolls provide suitable habitat for an important nest predator.

My findings of higher red squirrel occupancy rates at lower elevations (Figure 3.9) are likely responsible for the depression of nest survival and possibly fecundity since most failed nests were due to predation. Although the ecology of red squirrels in northeastern United States has not been adequately described (Vernes 2004), generally, their optimal habitat has been described as boreal spruce-fir forests (Stevens and Kennedy 1999). Spruce-fir forests are the dominant forest type across the sampled elevation gradient, yet I found a significant decline in red squirrel occupancy with increasing elevation (Figure 3.9). This finding implies that an environmental characteristic correlated with elevation other than habitat is affecting their occupancy rates. Low ambient temperatures at higher elevations may be responsible for the reduced occupancy rates of red squirrels I found at higher elevations (Anderson and Jetz 2005). If high elevations of northeastern North America continue to warm (Beckage et al. 2008, Seidel et al. 2009, Wright 2009), areas that currently provide refuge for breeding blackpolls from high red squirrel occupancy may be minimized causing lower nest survival and fecundity throughout the blackpoll's elevational distribution.

As the ecotone between the northern hardwood forest at low elevations and the montane spruce-fir forest shifts upslope (Beckage et al. 2008) in northeastern North America, there is evidence that potential competitors for breeding resources are also shifting upslope (Chapter 2). Specifically, six low elevation Parulids have shifted their upper elevational boundary approximately 117 m upslope between 1993 and 2009 and are increasingly overlapping with the elevational distribution of blackpolls (Chapter 2). Interspecific competition can be defined as the reduction in the distribution, reproductive performance or survival of a species that results from the shared use of a resource with

another species (Newton 1998). Although competition between Parulids has been documented in the region (MacArthur 1958) and blackpolls are less abundant (Figure 3.4) and experience lower reproductive success (Figures 3.5 – 3.8) within the elevational range of upward shifting Parulids, I cannot determine the extent to which interspecific competition affected those measures. This study did not directly test for consequences of increased interspecific competition on blackpoll reproductive performance. Future studies should directly assess the consequences of increased interspecific competition with low elevation species on montane bird reproductive performance. This is particularly important in light of the upward shift of suitable habitat and occupancy of low elevation competitors.

The general consensus is that montane spruce-fir forests in northeastern North America are predicted to shift upslope with future climate change (Rodenhouse et al. 2008) and this habitat will become increasingly fragmented and isolated. Historic evidence of this shift has been confirmed over the past 40 years with the 100 m advancement upslope of the northern forest ecotone with montane spruce-fir (Beckage et al. 2008). To date, scientists have only considered that the area of suitable habitat for montane species will decrease overtime with continued global warming. This is the first study to quantify the reproductive performance of a montane bird across an elevational gradient and document that habitat quality varies significantly across the elevation gradient. I provided evidence to suggest that across the elevational distribution of a montane bird, the low quality habitat at lower elevations is such that only a portion of the elevational distribution of this species is likely contributing to the overall population. Further work should be focused on determining the extent to which lower elevations

operate as population sinks and higher elevations as population sources for montane birds. What is clear is that as the hardwood forest ecotone continues to shift upslope, a higher proportion of the elevational distribution of montane birds will increasingly become low quality habitat.

Sufficient evidence exists to suggest that montane spruce-fir forest will encompass less of the landscape in northeastern North America with the continuation of climate change. The next step to understanding the consequences of climate change for the species that inhabit this ecological system is to begin to understand how they are performing in the habitat that is still present and to begin to connect that performance to variations in climate. My research is a critical contribution to this understanding. By considering some of the mechanisms by which variation in climate will affect montane birds, I have shed light on the immediate response of a montane bird to temporal variations in climate through breeding initiation and the indirect effects of the spatial variation in climate across an elevation gradient on habitat quality and ultimate blackpoll demography.

Table 3.1: A reproductive index modified from Vickery et al. (1992) used as an index of mate pairing success.

Rank	Description
1	Territorial male present 4 + weeks
2	Territorial male and female present 4 + weeks
3	Pair found nest building, laying or incubating eggs
4	Adults carrying food to presumed nestlings
5	Evidence of fledging success
6	Polygamous male with fledging success at both nests

Table 3.2: Parameter estimates for *N*-mixture models of blackpoll warbler abundance with ΔAIC_c <2 and the null model. Abundance (λ) covariates include elevation (E), a quadratic term for elevation (E^2) and year. Detection probability (*p*) covariates include wind, time of day, an index of weather and Julian date. Parameter estimates in bold have 95% confidence intervals that do not include zero. Data were collected along an elevation gradient ranging from 742 to 1,416 m asl in the White Mountain National Forest, NH in 2006 and 2007.

Abundance				Detection probability					ΔAIC_c	w^a	R^2
β 0	E	E^2	Year	β 0	Wind	Time	Weather	Date			
0.64	**0.30**	**-0.15**	0.16	1.97	**-0.23**	-0.01			0.00	0.37	0.26
0.64	**0.30**	**-0.16**	0.17	2.08	**-0.24**	-0.01	**-0.08**		0.46	0.30	0.25
0.63	**0.30**	**-0.16**	0.16	2.91	**-0.25**	-0.01	-0.07	-0.01	1.48	0.18	0.26
0.64	**0.30**	**-0.16**	0.15	2.75	**-0.27**	-0.01		-0.01	1.83	0.15	0.26
0.34				0.40					29.62	0.00	0.00

Table 3.3: Parameter estimates for single-season, single-species occupancy models of red squirrel occupancy with ΔAIC_c <2 and the null model. Elevation (E) is the occupancy (Ψ) covariate. Detection probability (p) covariates include temperature and Julian date. Parameter estimates in bold have 95% confidence intervals that do not include zero. Data were collected along an elevation gradient ranging from 742 to 1,416 m asl in the White Mountain National Forest, NH in 2007.

Occupancy		Detection probability			ΔAIC_c	w^a	R^2
β 0	E	β 0	Temp	Date			
9.78	**-.01**	-1.60	**-0.04**		0.00	0.33	0.33
8.91	**-0.01**	-3.96		**-0.03**	1.32	0.24	0.21
9.13	**-0.01**	**-4.27**	0.20	0.21	1.40	0.14	0.28
9.88	**-0.01**	**0.44**			1.64	0.12	0.02
0.55		**0.41**			33.22	0.00	0.00

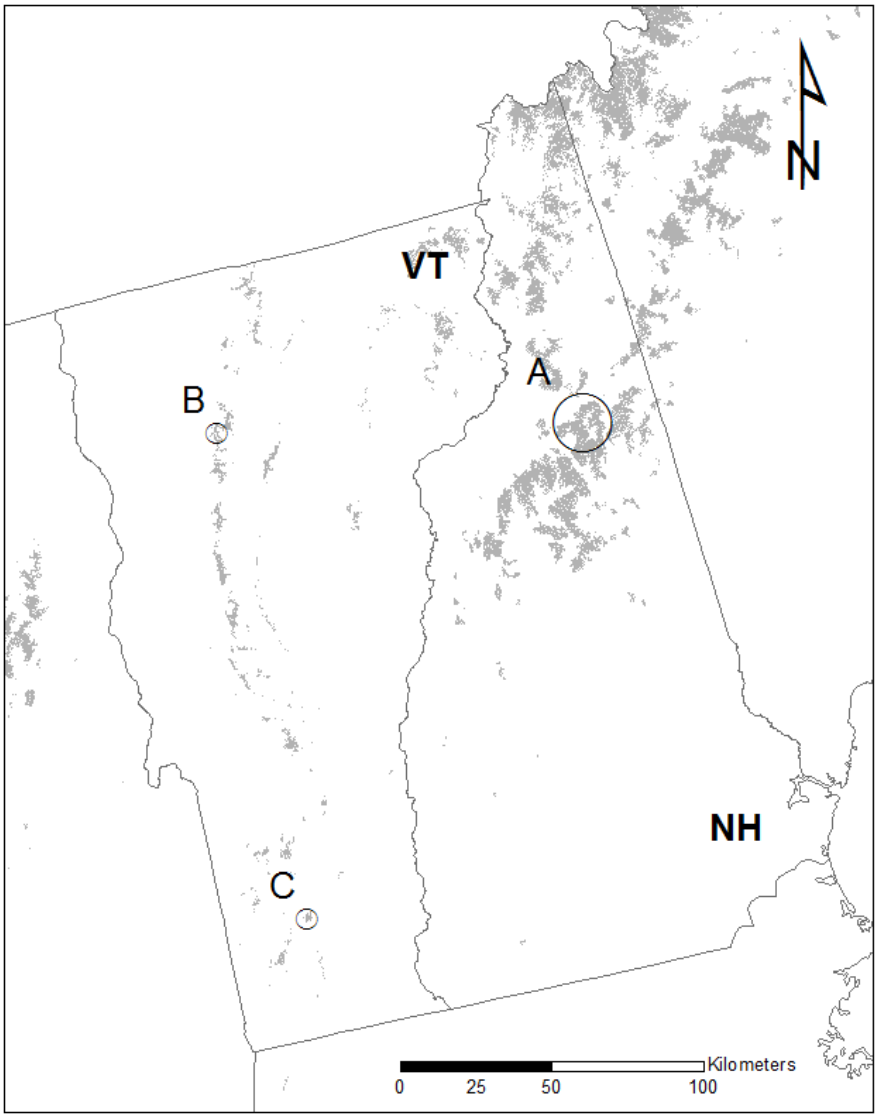

Figure 3.1: Distribution of montane spruce-fir forests throughout the Green (VT) and White (NH) Mountains. Study area A locates the Presidential Range and Mount Jefferson. Study area B identifies Mount Mansfield and study area C locates Stratton Mountain. Study area A was used to examine the effect of spatial climate variation on blackpoll warbler demography while study areas B and C were used to test whether temporal climate variation had an effect on blackpoll nest initiation and daily nest survival.

Figure 3.2: Male blackpoll warbler (*Setophaga striata*), Mount Jefferson, NH, June 2007.

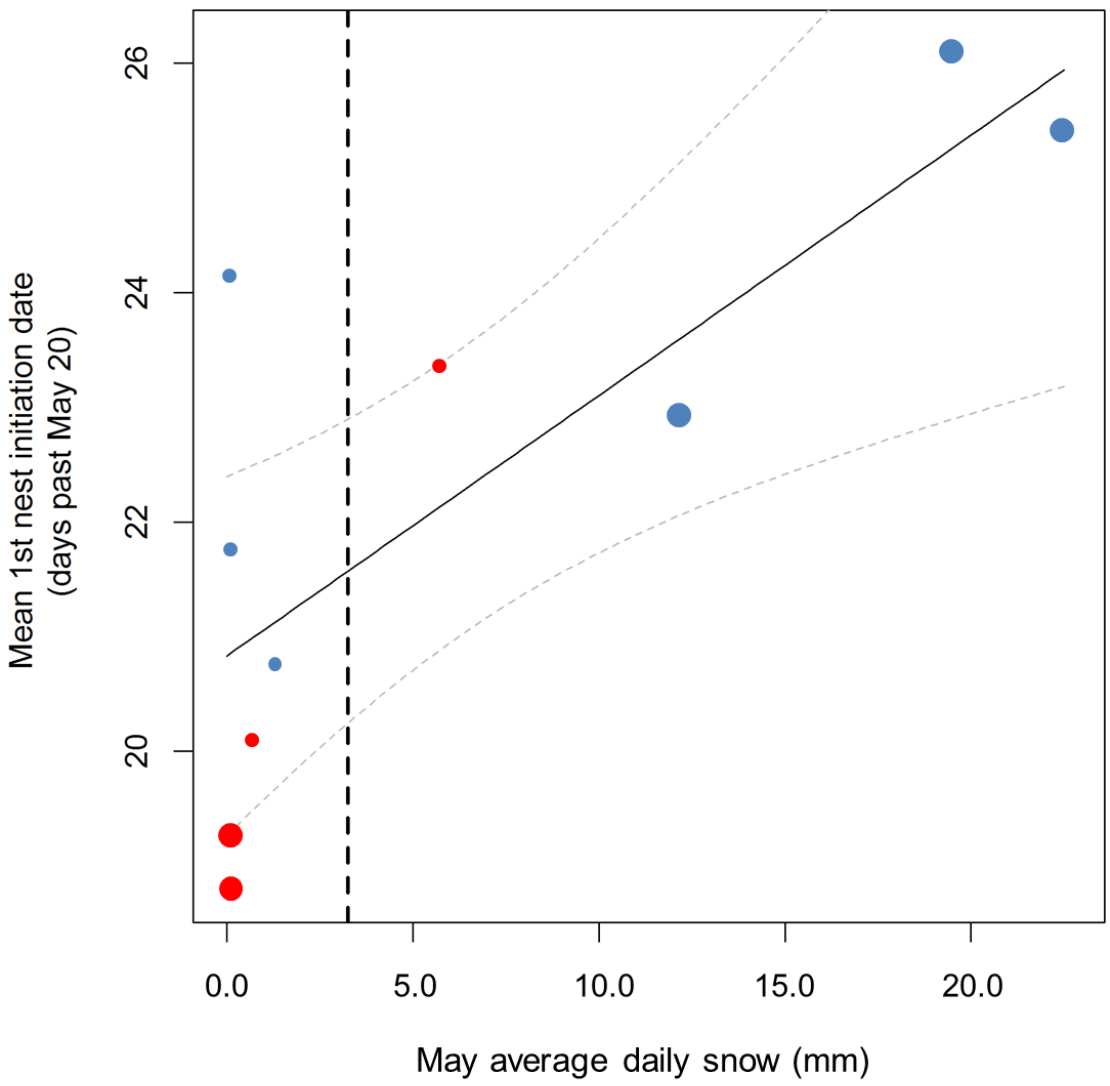

Figure 3.3: Ordinary least squares regression between May snowfall and blackpoll warbler nest initiation from 1994 to 2003. Blackpoll data were collected on Mount Mansfield and Stratton Mountain, VT. Climate data were collocted at the summit of Mount Mansfield. The dashed grey line is the 95% confidence interval of the regression line. The vertical dashed black line is the 55-year (1955-2010) mean daily snowfall in May. Blue data points are those with May maximum daily temperatures cooler than the 55-year mean and red data points are warmer than the 55-year mean. Large data points are >1 standard deviation from the 55-year temperature average and small points are <1 standard deviation from the 55-year temperature average.

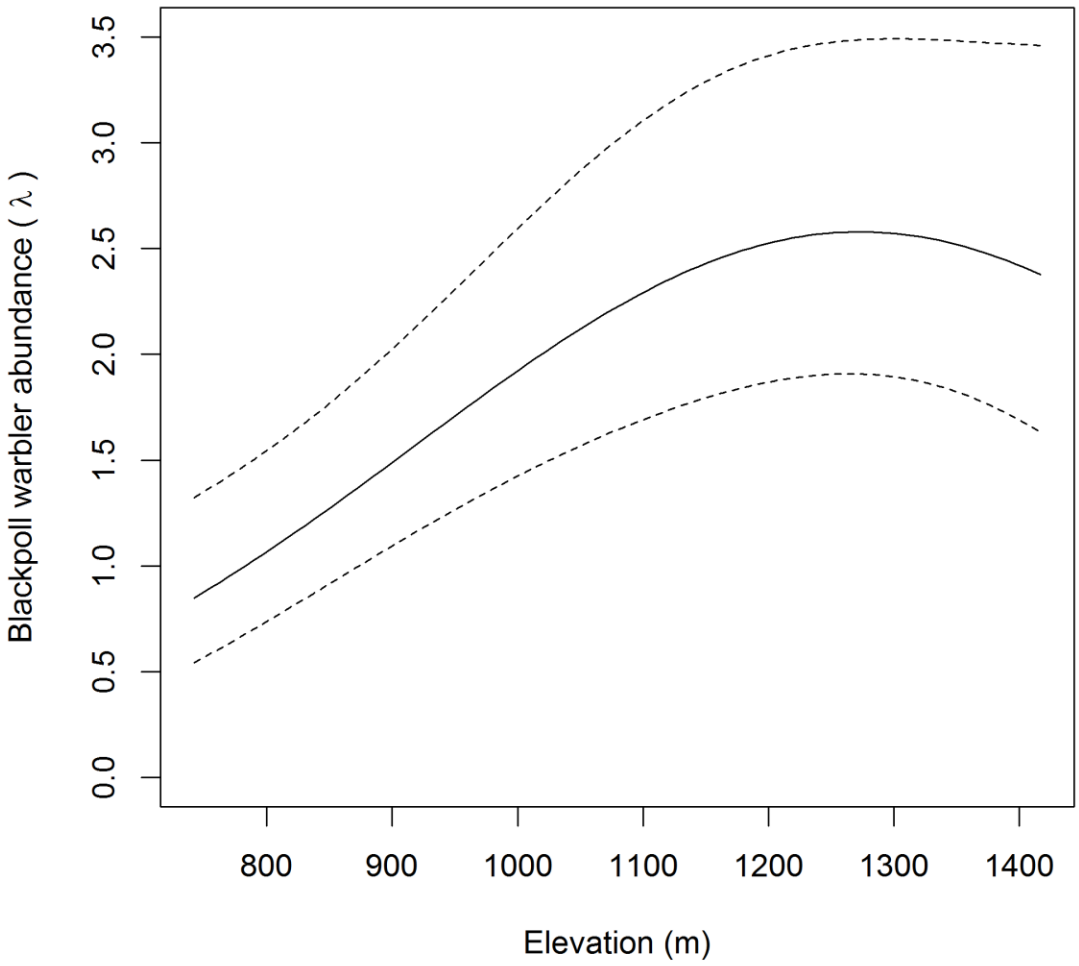

Figure 3.4: Blackpoll warbler abundance in relation to elevation in the White Mountain, NH, 2006 and 2007. Relationship was derived from an N-mixture model with greatest AIC_c support (Table 3.2), holding detection covariates constant at the mean. Error band is the 95% confidence interval.

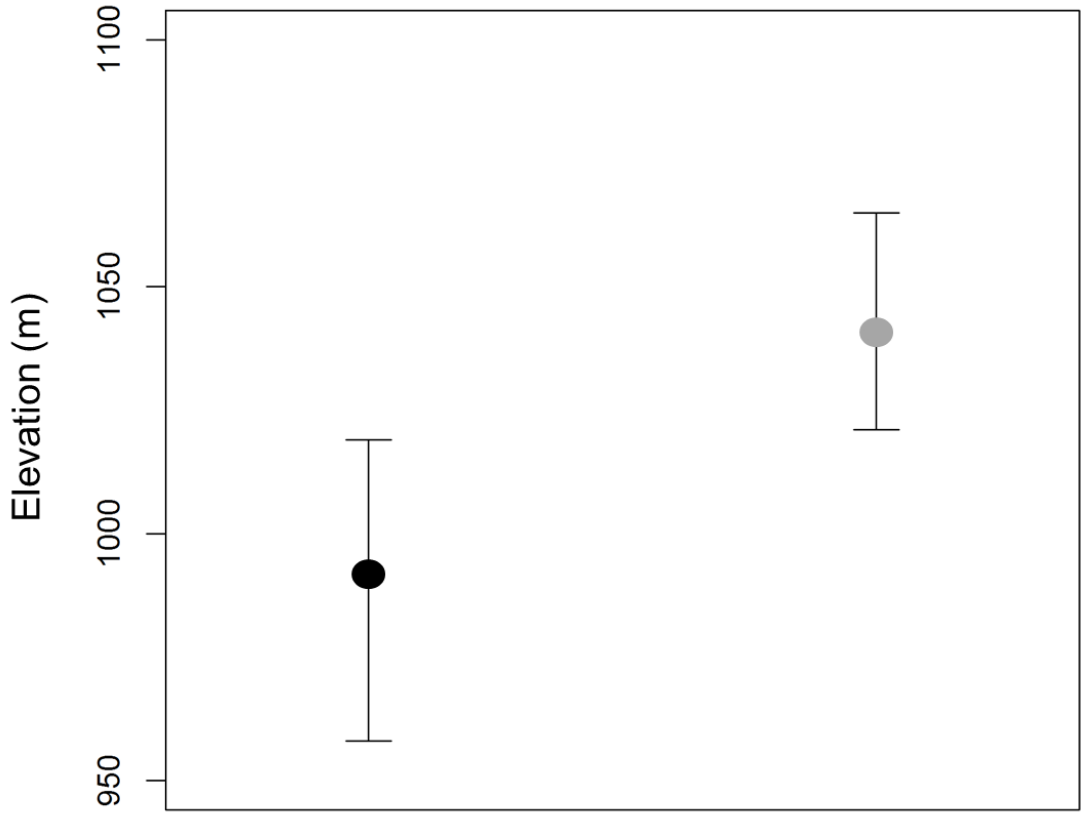

Figure 3.5: Mean elevation of 49 male blackpoll warbler territories for second year (black, mean = 992.5 m) and after second year (grey, mean = 1041 m). Error bars are 95% confidence intervals, which do not overlap. Data are from Mount Jefferson, NH, 2006-2008.

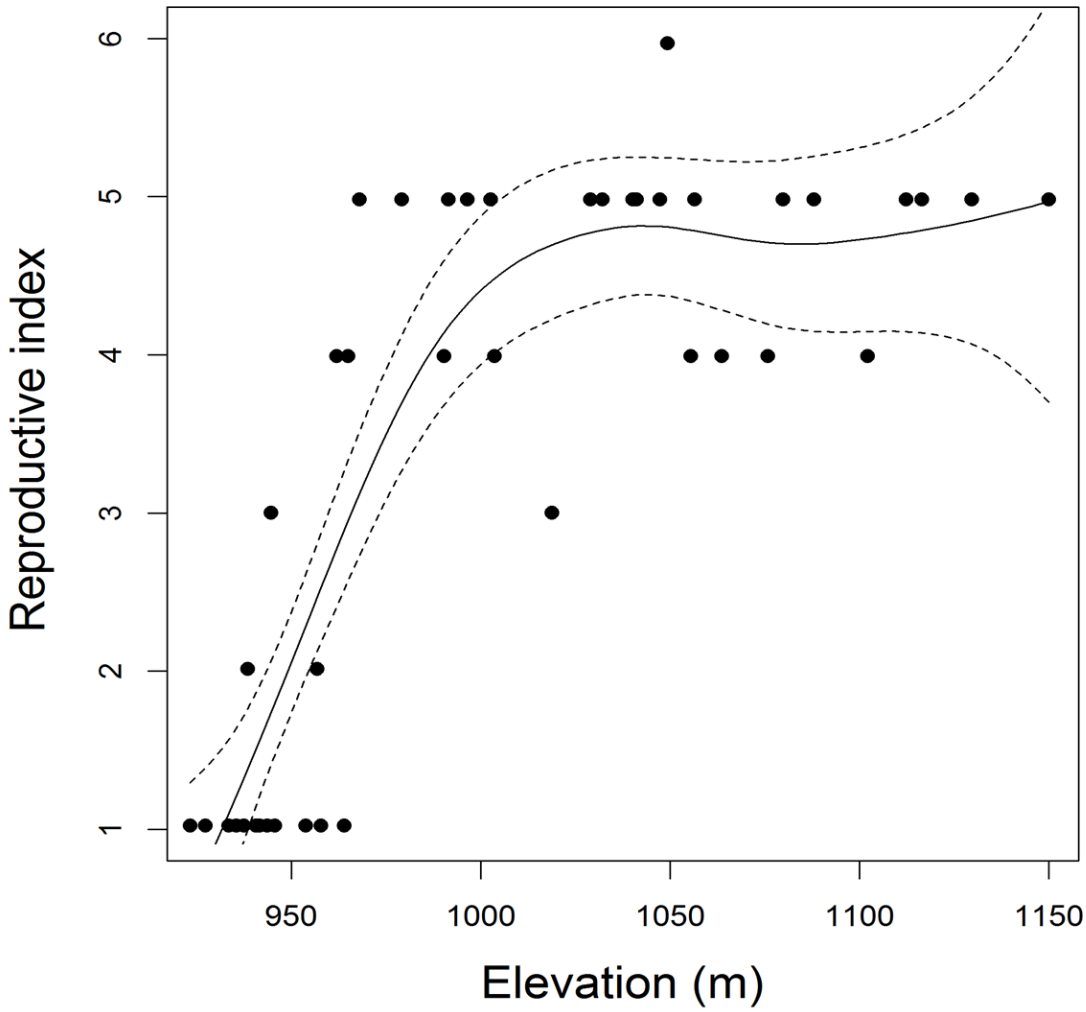

Figure 3.6: Blackpoll warbler pairing success as measured by a reproductive index in relation to elevation. The reproductive index scored 42 territories such that 1 = unpaired male; 2 = male and female, no evidence of breeding; 3 = pair with evidence of breeding; 4 = adults carrying food; 5 = evidence of fledging; 6 = male with two successful nests. Data were collected on Mount Jefferson, NH, 2007-2009.

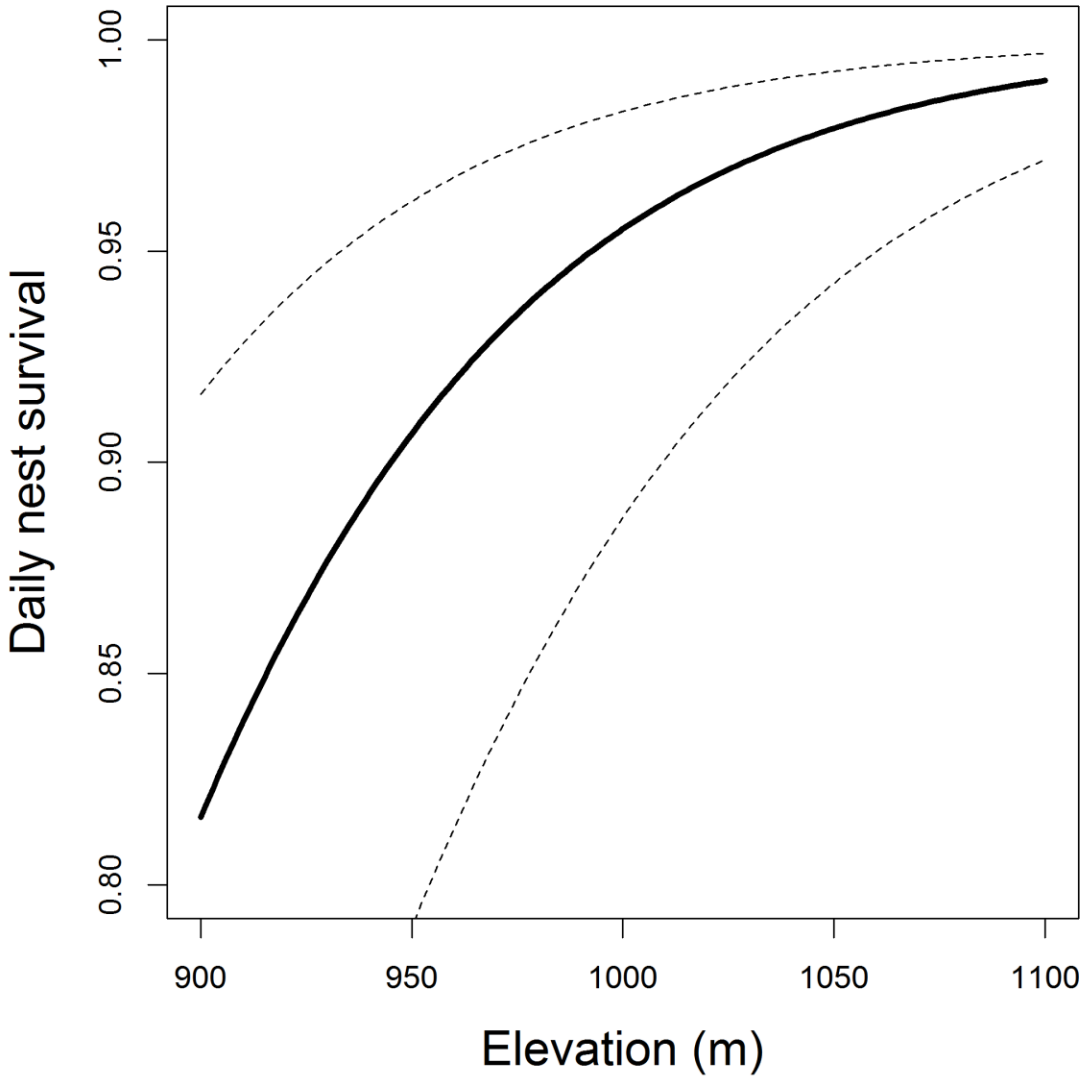

Figure 3.7: Blackpoll warbler daily nest survival across an elevation gradient estimated with a logistic-exposure model. Data are from 42 nests found on Mount Jefferson, NH, 2007-2009.

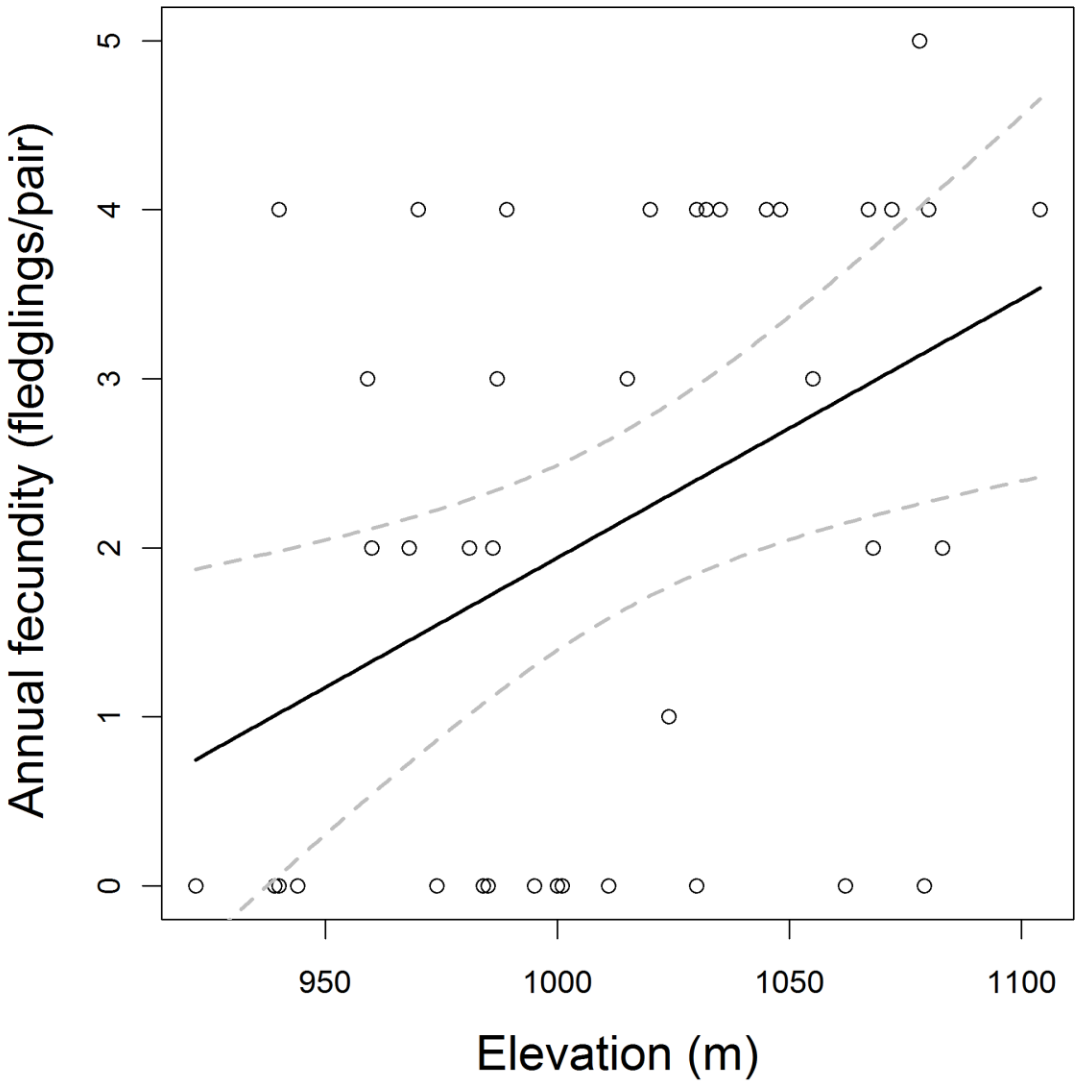

Figure 3.8: Ordinary least squares regression describing the relationship between blackpoll warbler annual fecundity and elevation for 42 nests on Mount Jefferson, NH, 2007-2009.

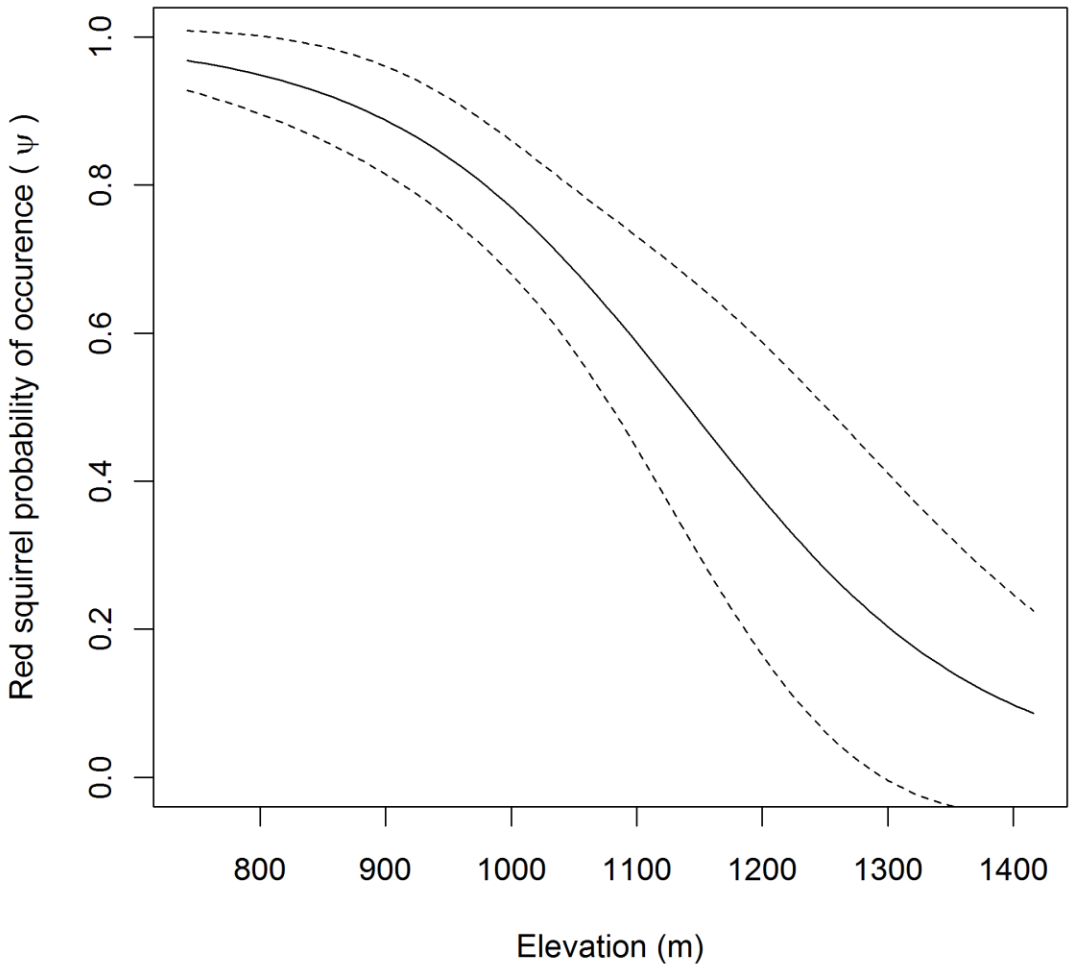

Figure 3.9: Red squirrel occupancy in relation to elevation in the White Mountain, NH, 2007. Relationship was derived from an single-season, single-species occupancy model with greatest AIC_c support (Table 3.3), holding detection covariates constant at the mean. Error band is the 95% confidence interval.

APPENDIX A

SPECIES DETECTED DURING POINT COUNT SURVEYS IN 2006 AND 2007 IN THE WHTE MOUNTAINS, NH

Common name	Scientific name	S	D	$\bar{x}$	Detection cue		
					song	call	visual
Blackpoll warbler*	*Setophaga striata*	473	773	1.269	488	3	282
Swainson's thrush*	*Catharus ustulatus*	377	645	1.059	339	174	132
White-throated sparrow*	*Zonotrichia albicollis*	284	415	0.681	272	10	133
Dark-eyed junco*	*Junco hyemalis*	304	410	0.673	232	48	130
Yellow-rumped warbler	*Setophaga coronata*	327	406	0.667	267	7	132
Yellow-bellied flycatcher*	*Empidonax flaviventris*	221	268	0.440	111	84	73
Winter wren	*Troglodytes hiemalis*	233	252	0.414	122	0	130
Black-throated green warbler	*Setophaga virens*	138	175	0.287	113	1	61
Magnolia warbler*	*Setophaga magnolia*	154	175	0.287	110	1	64
Red-breasted nuthatch	*Sitta canadensis*	128	160	0.263	2	151	7
Bicknell's thrush*	*Catharus bicknelli*	111	148	0.243	41	80	27
Pine siskin*	*Spinus pinus*	54	137	0.225	4	100	33
Golden-crowned kinglet	*Regulus satrapa*	96	106	0.174	38	28	40
Nashville warbler*	*Oreothlypis ruficapilla*	87	102	0.167	47	1	54
Boreal chickadee*	*Poecile hudsonicus*	63	72	0.118	14	33	25
Ruby-crowned kinglet	*Regulus calendula*	45	49	0.080	39	1	9
Blue-headed vireo	*Vireo solitarius*	39	43	0.071	31	0	12
American redstart	*Setophaga ruticilla*	33	41	0.067	27	0	14
Purple finch	*Carpodacus purpureus*	39	39	0.064	28	0	11
Black-throated blue warbler	*Setophaga caerulescens*	27	30	0.049	17	2	11
Black-capped chickadee	*Poecile atricapillus*	22	26	0.043	8	8	10
Red-eyed vireo	*Vireo olivaceus*	23	25	0.041	18	0	7
Cedar waxwing	*Bombycilla cedrorum*	8	19	0.031	7	8	4
Hairy woodpecker	*Picoides villosus*	19	19	0.031	1	16	2
Gray jay*	*Perisoreus canadensis*	11	17	0.028	10	4	3
White-winged crossbill	*Loxia leucoptera*	7	14	0.023	0	13	1

Brown creeper	*Certhia americana*	10	13	0.021	5	2	6
Ovenbird	*Seiurus aurocapilla*	11	13	0.021	9	0	4
Mourning dove	*Zenaida macroura*	10	11	0.018	2	4	5
Canada warbler	*Wilsonia canadensis*	7	10	0.016	8	0	2
Bay-breasted warbler*	*Setophaga castanea*	8	8	0.013	6	0	2
Black-backed woodpecker*	*Picoides arcticus*	7	8	0.013	0	5	3
Blue jay	*Cyanocitta cristata*	7	8	0.013	2	5	1
Hermit thrush	*Catharus guttatus*	7	7	0.011	4	1	2
Common raven	*Corvus corax*	6	6	0.010	0	6	0
American robin	*Turdus migratorius*	3	4	0.007	1	3	0
Red crossbill*	*Loxia curvirostra*	2	4	0.007	4	0	0
American crow	*Corvus brachyrhynchos*	2	3	0.005	0	3	0
Cape May warbler*	*Corvus brachyrhynchos*	2	2	0.003	0	0	2
American goldfinch	*Spinus tristis*	1	1	0.002	1	0	0
Black-and-white warbler	*Mniotilta varia*	1	1	0.002	1	0	0
Blackburnian warbler	*Setophaga fusca*	1	1	0.002	0	0	1
Common yellowthroat	*Geothlypis trichas*	1	1	0.002	1	0	0
Downy woodpecker	*Picoides pubescens*	1	1	0.002	0	1	0
Ruby-throated hummingbird	*Archilochus colubris*	1	1	0.002	0	1	0
Ruffed grouse	*Bonasa umbellus*	1	1	0.002	1	0	0
Scarlet tanager	*Piranga olivacea*	1	1	0.002	1	0	0
Sharp-shinned hawk	*Accipiter striatus*	1	1	0.002	0	0	1
Veery	*Catharus fuscescens*	1	1	0.002	0	0	1

APPENDIX B

RESULTS FROM LINEAR MIXED MODELS TESTING FOR CHANGES IN SEVERAL MEASURES OF SPECIES' ELEVATIONAL DISTRIBUTIONS BETWEEN 1993 AND 2009

Results are reported as the coefficient estimate, standard error, and total sample size, respectively. Bold indicates that the 95% CI of the coefficient does not include zero and that the coefficient is significantly different than zero ($P < 0.05$).

	Percentile of elevation distribution								
Species	0.1	0.2	0.3	0.4	Mean	0.6	0.7	0.8	0.9
Low elevation									
Least Flycatcher (*Empidonax minimus*)	-	-	-	-	-1.43 (4.94), 104	4.46 (5.29), 41	7.27 (4.25), 32	7.55 (5.56), 22	7.69 (7.51), 13
Black-capped chickadee (*Poecile atricapilla*)	-	-	-	-	**-2.77** (1.41), 232	**-4.10** (1.75), 92	**-5.08** (1.87), 72	**-8.39** (2.03), 49	**-9.63** (2.65), 27
Red-breasted nuthatch (*Sitta Canadensis*)	-	-	-	-	-0.50 (0.90), 445	0.004 (1.13), 178	-0.86 (1.30), 132	0.12 (1.49), 92	1.33 (1.84), 48
Brown creeper (*Certhia americana*)	-	-	-	-	-0.26 (2.24), 83	-0.43 (2.02), 34	-2.96 (2.25), 27	-0.45 (3.50), 19	-0.17 (4.52), 13
Ruby-crowned kinglet (*Regulus calendula*)	-	-	-	-	-0.64 (0.77), 452	1.04 (0.78), 181	0.98 (0.83), 135	1.21 (1.03), 92	-1.35 (0.98), 48
Golden-crowned kinglet (*Regulus satrapa*)	-	-	-	-	0.86 (0.85), 559	0.41 (0.82), 223	-0.12 (0.90), 168	0.21 (1.07), 114	0.01 (1.36), 60
Hermit thrush (*Catharus guttatus*)	-	-	-	-	**3.91** (1.82), 162	**8.27** (2.47), 63	**11.29** (2.57), 50	**14.29** (3.00), 33	**15.96** (4.43), 18
Red-eyed vireo (*Vireo olivaceus*)	-	-	-	-	0.70 (2.80), 62	-5.80 (3.16), 24	**-9.95** (4.35), 19	**-10.93** (4.69), 15	*

Blue-headed vireo (*Vireo solitaries*)	-	-	-	-	0.65 (1.28), 150	-1.42 (1.87), 59	0.20 (2.24), 47	-0.17 (2.54), 33	-0.65 (3.41), 19
Black-throated green warbler (*Setophaga virens*)	-	-	-	-	1.07 (0.78), 434	**2.69** (1.05), 173	**2.94** (1.15), 133	**4.26** (1.47), 89	**6.00** (1.79), 47
Black-and-white warbler (*Mnioilta varia*)	-	-	-	-	**11.53** (2.75), 63	**19.25** (3.00), 24	**18.29** (3.28), 20	**16.11** (4.90), 14	**17.30** (6.16), 10
Black-throated blue warbler (*Setophaga caerulescens*)	-	-	-	-	**4.85** (1.79), 81	**11.39** (2.05), 31	**10.85** (2.19), 26	**12.92** (2.77), 17	**12.25** (3.77), 13
Canada warbler (*Wilsonia canadensis*)	-	-	-	-	**9.37** (4.58), 31	**17.12** (5.45), 12	**16.23** (5.81), 11	**15.62** (7.08), 8	*
Blackburnian warbler (*Setophaga fusca*)	-	-	-	-	**10.66** (2.70), 69	**14.27** (2.38), 28	**13.79** (3.08), 22	**14.91** (2.70), 18	**13.67** (3.98), 12
American redstart (*Setophaga ruticilla*)	-	-	-	-	**8.16** (2.14), 131	**14.03** (2.70), 53	**14.42** (2.83), 42	**13.35** (2.94), 20	**19.26** (5.41), 19
Ovenbird (*Seiurus aurocapillus*)	-	-	-	-	**5.31** (2.32), 42	5.90 (3.25), 17	7.27 (4.05), 14	**9.79** (3.31), 11	**9.29** (3.99), 10
High elevation									
Magnolia warbler (*Setophaga magnolia*)	-0.35 (0.62), 120	-0.36 (0.45), 230	-0.52 (0.39), 345	-0.61 (0.37), 457	0.48 (0.53), 1145	0.20 (0.60), 456	0.36 (0.64), 345	**1.78** (0.76), 229	**2.57** (1.01), 119
Swainson's thrush (*Catharus ustulatus*)	**-2.07** (0.55), 194	**-2.06** (0.44), 382	**-1.86** (0.40), 572	**-1.73** (0.39), 757	-0.40 (0.52), 1897	-0.31 (0.55), 759	-0.23 (0.53), 571	0.33 (0.56), 381	0.87 (0.65), 193
Winter wren (*Troglodytes troglodytes*)	**-1.33** (0.46), 281	**-1.52** (0.38), 559	**-1.33** (0.37), 838	**-1.23** (0.35),	**-0.89** (0.44),	**-1.27** (0.38),	**-1.05** (0.39), 839	**-1.01** (0.43), 560	**-1.00** (0.46), 282

				1116	2792	1116			
Yellow-bellied flycatcher (*Empidonax flaviventris*)	-0.70 (0.55), 183	**-1.07** (0.43), 359	**-1.42** (0.41), 539	**-0.98** (0.38), 713	-0.36 (0.47), 1788	**-1.86** (0.46), 713	**-1.60** (0.48), 538	**-1.28** (0.51), 358	**-1.38** (0.67), 183
Nashville warbler (*Vermivora ruficapilla*)	**-1.53** (0.62), 59	-1.41 (0.73), 109	-0.98 (0.63), 163	**-1.19** (0.58), 216	-0.46 (0.86), 539	**3.46** (1.10), 216	**3.05** (1.27), 163	**3.64** (1.58), 111	3.18 (2.19), 59
Blackpoll warbler (*Setophaga striata*)	**-0.71** (0.34), 412	**-1.04** (0.29), 820	**-1.03** (0.28), 1226	**-0.79** (0.26), 1633	-0.12 (0.30), 4084	0.07 (0.26), 1629	0.20 (0.27), 1226	0.17 (0.29), 820	0.57 (0.30), 413
Yellow-rumped warbler (*Setophaga coronata*)	**-0.87** (0.39), 318	**-1.13** (0.35), 634	**-0.98** (0.34), 946	**-0.91** (0.33), 1260	-0.06 (0.36), 3150	0.02 (0.30), 1260	-0.19 (0.32), 946	0.05 (0.34), 632	0.11 (0.37), 319
Boreal chickadee (*Poecile hudsonicus*)	0.14 (1.66), 55	0.03 (1.25), 104	0.26 (0.99), 155	0.25 (0.83), 205	0.28 (0.73), 513	0.59 (0.72), 205	0.61 (0.83), 155	-0.22 (0.91), 104	-0.63 (1.02), 55
White-throated sparrow (*Zonotrichia albicollis*)	0.16 (0.38), 310	-0.43 (0.35), 611	-0.43 (0.35), 914	-0.05 (0.34), 1215	0.19 (0.37), 3038	-0.11 (0.31), 1214	-0.24 (0.33), 912	-0.55 (0.33), 611	**-0.68** (0.33), 308
Bicknell's thrush (*Catharus bicknelli*)	-1.09 (0.98), 98	-0.78 (0.77), 189	-0.75 (0.66), 282	0.31 (0.62), 374	0.12 (0.60), 932	0.56 (0.52), 374	0.55 (0.53), 282	-0.01 (0.52), 189	0.85 (0.72), 93
Dark-eyed junco (*Junco hyemalis*)	**-1.88** (0.53), 232	**-1.64** (0.45), 458	**-1.21** (0.42), 684	**-1.05** (0.43), 909	-0.75 (0.48), 2275	-0.33 (0.37), 906	-0.23 (0.39), 684	-0.23 (0.39), 458	0.08 (0.41), 233

*Models were not run because number of random effect grouping levels was equal to observations.

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